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VOLUME 13 JANUARY, 1939 NUMBER 1

SILICEOUS SPONGES FROM MISSISSIPPIAN AND DEVONIAN STRATA OF THE PENN-YORK EMBAYMENT

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Cincinnati, Ohio

ABSTRACT—New siliceous sponges from the Mississippian and Devonian strata of the Penn-York Embayment of the Allegheny Plateau are described: from the Oil Lake series, a new family, genus and species, Titusvilliidae, *Titusvillia drakei;* a new species of dictyosponge, *Calathospongia tidioutensis,* is also described. The holotype of the last species bears on the internal mold the imprint of an ophiuroid echinoderm which presents an interesting problem. An occurrence of *Calathospongia carceralis* in the Tidioute shale of Pennsylvania is also recorded. New dictyosponges from the Devonian are described: in the Venango stage of the Conewango series a new subfamily, genus, and species, Corticospongiinae, *Corticospongia bradforddensis,* and from the Enfield stage of the Senecan series, the new genus and species *Ithacadictya cornelli* (Dictyospongiinae), are described. All of the new forms appear to come from the same general facies zone as most of the hitherto described siliceous sponges from New York and Pennsylvania.

SYSTEMATIC DESCRIPTIONS

PORIFERA

Class HEXACTINELLIDA Schmidt

Order LYSSACINA

Family TITUSVILLIIDAE Caster, n. fam.

A FAMILY of thick-walled hexactinellid sponges in which three definite zones of spicular differentiation are present in the mesogloeal region: these are an external or so-called epidermal semi-net, a subsurficial mat and a paragastric net. A more or less complete reticulum is present at each zone, and dissociated spicular elements are present throughout the sarcode zone. A branching, supercolonial mode of life is an additional unique characteristic of the family. Inasmuch as the family is monotypic at the present state of our knowledge, it is assigned the additional characters of the new genus and species *Titusvillia drakei,* below.

TITUSVILLIA Caster, n. gen.

This is a new genus of siliceous sponge, which has the attributes of the new family Titusvilliidae outlined above, some refinements of which are apparently of generic significance. All parts of the supercolony are made up of cuplike nodes, the orientation of which varies within the colony, and all of which are connected by a central cloacal or paragastric cavity; branches leave the main zigzag axis in a spiral manner at about 120° intervals. Surface of external mold reticulate. Additional characteristics are brought out under the specific analysis which follows.

Genotype, *Titusvillia drakei* Caster, n. sp.

TITUSVILLIA DRAKEI Caster, n. sp.

Plate 1, figures 1–4; plate 2, figures 1–5; plate 4, figure 7; and text figures. 1–3, 8

Species having the characteristics of the

new family and genus outlined above and the structural features shown on the plates and text figures. Of apparently specific significance are the detailed characteristics of the attributes assigned to the family and genus. These embrace gross anatomy, including mode of colonial growth, wall relationships, including details of the spicular patterns, and the dimensions of the various parts.

The supercolony consists of a zigzag axis of cuplike nodes from which unbranched arms (colonies) of the same diameter as the axis radiate spirally at about 120° intervals, but with upwardly decreasing pitch to the spire. This is brought out by the drawing, text fig. 8, and by the photographs, where the main, parental, or axial, colony or colonies are designated in astogenetic sequence, A-1, A-2, A-3, and A-4; and the branches or individual secondary colonies are in the same sequence numbered I to V. It may be observed that there are 8 cups in the holotype on the axis (A-1) prior to the first branch (I) (there is good evidence that there were actually 10 or more cups in life) but there are only 3 or possibly 4 cups on the A-2 section prior to branch II, and 4 cups between branches II and III, and only 2 or possibly 3 cups prior to the final branching. The colonial rami show no evidence of branches on the specimens at hand. All parts of the supercolony show a sinuous serpentine growth.

The cups are of essentially the same size throughout all the colonies but show a wide variety of shapes. First, the A-1 and A-2 parts of the axial colony and the branches derived therefrom have the cups upwardly directed, as the specimen is oriented in the drawings, whereas the later parts of the axis, A-3 and A-4 and their branches have all the cups inverted in relation to the lower ones. One possible interpretation of this is given under Discussion, below, and illustrated by text figure 3. This may be an environmental tropism. Polytropism is one of the most characteristic attributes of the Porifera both living and fossil.

Each cup, which corresponds to an individual sponge, consists of a constricted concave or cylindrical base or neck, which becomes explanate or even convex as it is expanded to form a cover to the adjacent expanded cup; in the opposite direction the constricted neck expands relatively rapidly, the while becoming convex or planate to form the swollen body of the cup. Over the whole colony the relative proportions of neck to body of the cups is about as one to two; the length of the cups averages one-half the maximum width but is highly variable. Peripherally the body of the cup is usually very slightly constricted into a rounded edge, which rises as a keel or flange above the submerged cover area; the keel is sometimes acute and apparently always bore a marginal fringe of upwardly directed prostalial spicules. In individual cups the flange, together with the marginally attached cover or lid, is incurved to a considerable degree. The lid or cover is usually broadly concave around the margin of the cup and less so toward the axis; some cups show evidence of at least one circle of perforations just within the margin of the lip; these apparently were the openings of axially directed canals, which extended into the interior of the sponge. As can be seen by the illustrations, several of the cups show a tendency to develop a circuitous external groove or depression on the most expanded part of the cup. Cups of this type recall the duplex nodes on the dictyosponge genus *Ceratodictya*. This tendency, while apparently present occasionally in all parts of the colony, is most pronounced on the A-1 part of the axis. This may be of phylogenetic as well as astogenetic significance. The periphery of the cups is always sigmoidal or broadly lobate as the illustrations bring out.

The mode of origin of the colonial branches, which appear to be distinct colonies, the whole being a colony of a higher order, seems to have been by lateral gemmation in all of the branches where it can be studied. The drawing, text fig. 8, very faithfully represents the external characteristics of the holotype. Neither the base of the supercolony nor the distal termination of any of the colonial arms is known. It is assumed, however, that the aperture was constricted and corresponded in mature individuals (cups) to the narrowest diameter of the cup whatever the orientation of any particular branch may have been. It is probable, without proof, that the osculum lacked a sieve plate and bore peripheral

prostalial spicules of the type shown on branch II, text fig. 8. Certainly in the holotype there are no relict sieve plate diaphragms across the tubes.

As indicated under the generic analysis, the wall (presumably chiefly mesogloeal) of this sponge was very thick and bore several zones of spicular concentrates, each with a more or less complete hexactinellid reticulum, as well as a multiplicity of associated spicules, generally too poorly preserved to be described. There is also some evidence of the presence mesially of a weak space-lattice arrangement of the hexactins such as characterize the Dictyonina and are supposedly absent from the Lyssacina. This will be taken up in greater detail under Discussion, below.

It is assumed that the spicule-producing cells (scleroblasts) of this genus, as in the usual sponges of this type, were chiefly restricted to the mesogloeal or "sarcode" zone, and that no evidence of the ectodermal (and epidermal) tissue is preserved in the fossil. What remains consists of the impression of an external ("epidermal") basket or semireticulum, which is uniformly separated from the "internal mold" or inner filling of mud and sand by a zone of delicately fibrous or matted limonite, which was apparently derived from pyrite or marcasite. The former mineral most frequently replaces spicular material everywhere in the Penn-York Embayment, as Hall and Clark (1898) point out. The weathering away of the limonitic mat leaves a cavity between the external mold and the internal fill. (See plate 1, figures 3, 4; plate 2, figures 1, 2, 4, 5.) The surface of the sandstone filling is finely reticulated but in a somewhat different pattern from the semireticulum of the surface. There seem also to be space-lattice fragments all through the inner fill when it is broken open or eroded. Finally, there is present throughout the supercolony a mud-filled inner tube, which bears externally a fine, even reticulum. This inner net is closely similar to the usual reticular pattern of the Dictyospongiidae and is for the present viewed as the true paragastric reticulum. These relationships of the fossil are brought out by text figures 2 and 8. The reticular detail of the various zones is shown in diagram by text figure 1.

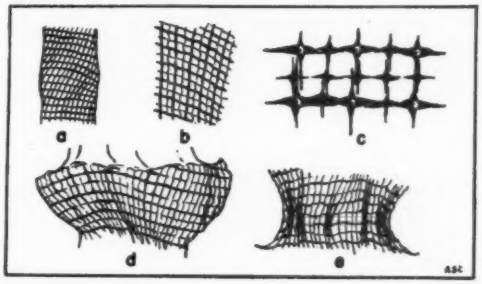

FIG. 1.—Reticular detail of the holotype of *Titusvillia drakei* Caster, n. sp. *a*, Paragastric reticulum, whose mesh usually measures less than 0.5 mm on a side and shows little or no graduation into quadrules and meres; the vertical elements are consistently spiralled about the tube; drawn from the distal part of branch IV. *b*, Exceptionally fine preservation of the paragastric net on the distal part of branch V; primary quadrules approximately 1 mm on a side are outlined by primary spicular bands; the quadrules are subdivided into meres. *c*, Apparent external ornamentation of the hexactins constituting the external semireticulum, drawn from an impression of the surface at the terminus of branch V; the axis of each primary hexactin is reduced to a mere boss at the junction of the swollen radii; the horizontal elements more nearly coincide to form spicular bands than do the adjacent vertical elements, thus giving wavering, indistinct vertical and relatively regular horizontal components; the same condition evidently prevails in the secondary spicules. *d*, A small area of the surface reticulum illustrating the gross effects of the structural detail shown in *c;* drawn from the ninth cup distad of the junction on branch V. *e*, Crowding of spicules on the constricted necks of the cups, resulting in very pronounced bundles of vertical radii; the horizontal radii in this area are of average size but appear smaller by contrast; the semireticulum is also slightly corrugated along the axes of these prominent bands; drawn from the eighteenth cup distad of the junction on branch V.

As shown on plate 4, figure 7 and by text figure 1, *c*, *d* and *e*, the surface reticulation as a whole consists of primary quadrules, which are subdivided once into meres. The reticular hexacts are mesially much swollen, and the horizontal surface radii are usually the more prominent. The resulting horizontal spicular fascicles are considerably more prominent than the vertical over most of the surface. The vertical spicular bands vary in thickness and are often evanescent and

wavering, as though the vertical radii of adjacent hexacts failed to meet precisely and varied in the degree of their alignment. The horizontal bands are also slightly undulatory. The general size of the primary quadrules averages 0.5 to 0.75 mm on a side where the surface was essentially flat. The vertical components appear to be slightly convex outward between horizontal bands, thus giving a curious differentially shrunken or constricted (seersuckerlike) appearance to the surface. The proportions of the quadrules vary with the surface form of the cups. Especially noteworthy in this connection is the crowding on the necks of the cups, which brings the elsewhere weak vertical components into prominence as swollen bands in the narrowest zone where the greatest consequent mechanical support is needed. This phenomenon is brought out by text figures 1, *e* and 8 as well as by the photographs. It appears that the horizontal radii of the hexacts are shortened in this constricted zone, and the vertical ones strengthened, in addition to the crowding out of existence of some of the primary quadrules and the resultant formation of superfascicles. The horizontal bands appear weaker only by comparison; actually they are of usual strength. The entire reticulum also appears to be vertically pleated along the axes of the vertical bundles, thus adding to the colony the slight additional strength of corrugation. The secondary spicules of the surface appear to follow the same general plan as the principal ones. The drawing, text figure 8, catches the minutely rugose aspect of the surface reticulum very well. This rugosity is slightly increased by the presence of small bosses or knobs at the junction of the vertical and horizontal bands of the primary quadrule. These have been thought of as the relict portions of external vertical radii of the principal hexacts. This surface rugosity is shown to a slight degree by plate 4, figure 7.

The space between the outer mold and the inner fill has been described as occupied by a limonitic spicular mat or else by a cavity in the holotype. The inner fill does not precisely conform to the contour of the outer mold, as the diagram in text figures 8 and 2, *b* bring out. (See also plate 2, figures 2 and 3, and plate 1, figure 4.) The spicular mat was thickest (where now the space is widest) at the angle of the cups. The limonite mat is too fragile and the preservation too poor in the specimens at hand to make any analysis of the spicules possible, but rods, clemes and acicular spicular elements seem to be present. The general nature of the mat is shown on figure 7, plate 4. The

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EXPLANATION OF PLATE 1

FIGS. *1–5*—*Titusvillia drakei* Caster, n. gen., n. sp. Holotype no. 22130, University of Cincinnati Museum, from the Tidioute member of the Cussewago stage in the Oil Lake series (Mississippian) in Church Run, at the Titusville Public School, Titusville, Pennsylvania. Compare with Text fig. 8, for relationship of pictures to complete specimen. (p. 1)

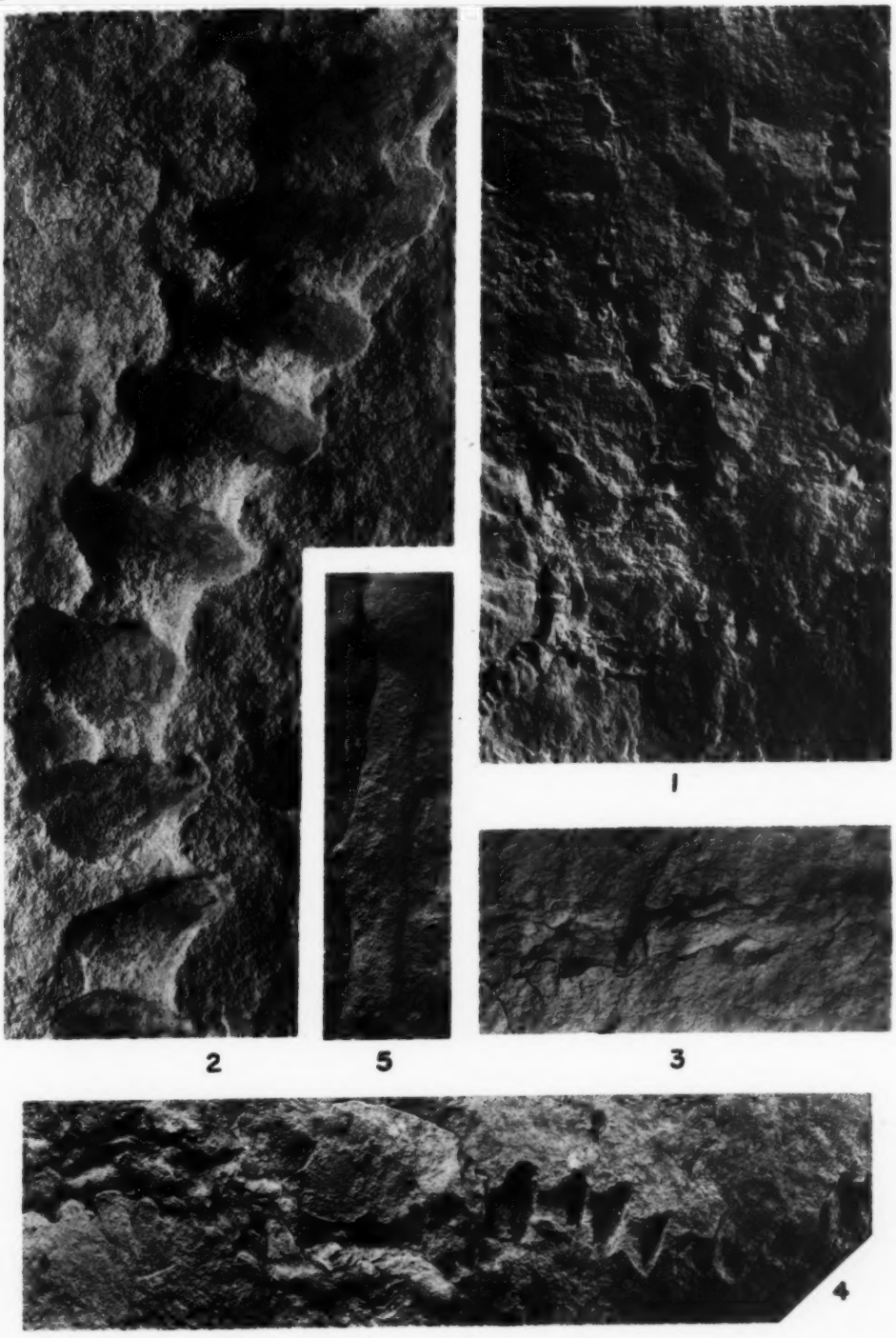
1—Attitude of the colony on the holotype slab, oriented to show most of the axial part and all of the branches. ×¾.

2—Enlargement of the external mold of the mesial part of branch V to show weak development of vertical components of the surficial semireticulum, the flange of the cups, and the variability in the size and proportions of the cups. Photograph purposely inverted to give the optical illustion of convexity to the picture. These are inverted cups on the original specimen. ×2½.

3—Mesial portion of branch IV showing the outline of several cups, with peripheral extensions suggesting tufts of spicules; the discordance between the inner filling and the outer mold is shown here, and also the slight crumpling of inner filling around the zone of the paragastric tube, which is here laterally displaced. ×¾.

4—Distal part of arm III, a variety of cup impressions, the inner filling and zone of limonitic spicular mat. In the middle of the photograph the paragastric tube is exposed and here has been forced out of the main axis of the colony. Its circuitous course can be traced in the inner fill toward the left. ×1.

5—Enlargement of the continuation of the paragastric tube shown at the middle bottom of figure 4. Further preparation after figure 4 was made showed the tube continuing for about 35 mm outside the axis of the main colony tube. This figure shows the faint impressions of the paragastric reticulum, which covers the entire surface, and also the position of four of the slight nodular expansions of the tube with the circles of low tubercles at each. ×2½.



Caster, Paleozoic Sponges

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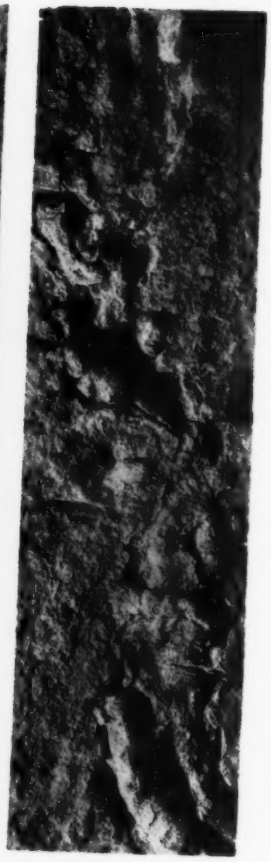

2

3

4

5

Caster, Paleozoic Sponges

peripheral spicules shown on some of the cups of text figures 8 and 2, *h* apparently originated in the matted zone. This mat may well represent a more or less "felted" skeletal element, which made possible the upright growth of such extraordinarily long branches as the holotype shows.

The surface of the inner mold is indistinctly reticulated, but no definite division into quadrules and meres has been observed. It appears to be on the whole a rather regular net or lattice, the surficial part of which has a net-like appearance, meres measuring about 0.5 mm on a side. There is some suggestion in places of a very irregular pattern of spicular elements such as the inner surface of a spicular mat would have presented to the infiltrating mud. The spicules that are present throughout the mud fill of this space, which in life appears to have been the chief mesogloeal zone, are too delicate to make definitive statements possible. Certainly there was not a regular meshwork throughout the space after death that would hold the inner paragastric net in a fixed position, for the tubular inner reticulum is often eccentrically situated and in at least one case has been forced free of the two inner spicular zones for a short distance (plate 1, figures 4 and 5).

The paragastric tube is shown in several of the photographs, e.g., plate 2, figure 2, and the net in detail by text figure 1, *a*, *b*, and plate 1, figure 5. The reticulations of this net are as fine or finer than the sand grains filling it and have proved so far almost impossible to catch by photograph. They are however, almost uniformly developed wherever the paragastric filling is exposed, and can be caught with a hand lens in very direct lighting. The reticulum consists of a very fine net having meres about 0.5 mm on a side, which occasionally shows evidence of subdividing a primary set of quadrules about 1 mm on a side. In regularity of pattern and general aspect this net more strongly recalls the usual dictyosponge net than any other structure seen in the present fossil. The vertical strands everywhere tend to spiral about the tube. The paragastric tube is of approximately half the major diameter of the cups at their widest part, or even a little less. It is only very slightly expanded in the upper central part of each cup, i.e., in the most expanded part of the cups, and this expansion appears to be slightly tubercular in a ring situated on the upper surface of the greatest expansion. The arrows on figure 5, plate 1, indicate the position of four of these rings. The tubercles of the filling are quite irregular and not infrequently obscure, but on the whole appear to be tiny cones with their narrow ends directed upwardly and outwardly toward the peripheral surface of the cup covers, essentially toward the circle of apertures suggested on the covers just inside the periphery. These tubercles of the paragastric

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EXPLANATION OF PLATE 2

FIGS. *1–5*—*Titusvillia drakei* Caster, n. gen., n. sp. Details of the holotype specimen to show generic and specific characters. Compare with text fig. 8 for the relation of these photographs to the entire specimen. (p. 1)

1—Junction of the most distal reversed branches, IV and V. Note the variability of the cups in branch IV, on the right; the cup 30 mm from the junction on branch IV shows very clearly the profile of what is termed a "duplex" tendency; on branch V the fourth cup from the junction shows some of the horizontal striae rather clearly in the half shadow. The meaning of the crumpling in the upper middle of the picture is unknown and has not yet been connected with the present fossil. Enlargement of the mesial part of branch V shown on plate 1, figure 2. ×1.

2—Proximal part of branch I, showing in the lower right part of the sigmoidal paragastric tube, which can be traced throughout the fill for the entire length of the photograph. The discordance between the fill and the external mold is also well shown here. The reticulations on the paragastric tube show faintly in the lower right. ×1¼.

3—Basal external mold, *A-1*, of the colony with its curious duplex folds on some of the cups and highly variable form of the nodes. ×1.

4—Distal part of branch V, inverted; the fringe of peripheral spicules is shown here in profile in the middle cups of the photograph, and in the upper left the paragastric tube breaks through the inner fill. ×1.

5—The *A-3* section of the axis at the place where branch III leaves the main colony. The inverted cups of the axis and the branch show well here. ×1.

filling are interpreted as the axial parts of a radial series of tubules, possibly inhalent in function, which lead from the exterior to the central cavity, and were apparently lined by spicules of a finer sort than those on the paragastric wall (canalaria?). So far as known, there were no diaphragms across the colony tubes, and all of these spicular reticula and mats were perfectly continuous throughout the colony, as was the paragastric cavity. These relations are brought out in text figure 2.

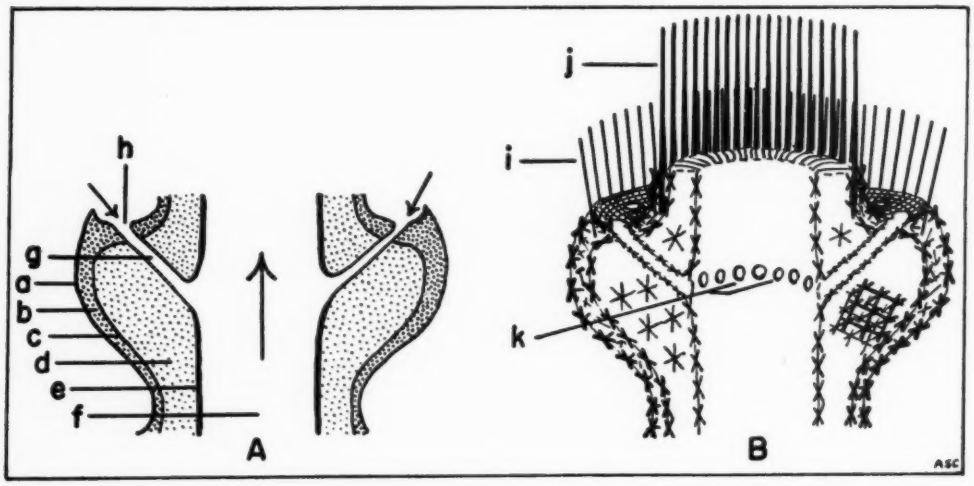

FIG. 2.—Idealized vertical section through *Titusvillia drakei*. All structures inferred from the holotype material. All proportions exactly as in the holotype. *A*, Generalized relationships of the walls of the sponge. *B*, Inferred distribution of spicules over the parts shown in *A*. *a*, External skeletal semireticulum of suppressed hexactins ("epidermal" skeleton). *b*, Outer limonitic zone of the fossil, which represents a pyritized spicular mat, which was probably the chief supporting skeleton for the sponge. *c*, Surface of the "inner mold" of the fossil, which presumably represents the beginning of the free jelly zone of the mesogloea in life; this is consistently indistinctly reticulated and marked by spicular impressions on the surface and contains scattered spicules throughout, some of which suggest a frail "space-lattice" dictyonalia. *d*, The main mass of the inner filling, which occupies the vacated area formerly filled with mesogloea and tubules. *e*, Paragastric reticulum at the contact of the mesogloea and the endodermal tissue, presumably, composed of biaxial hexacts; comparable to the reticulum of the Dictyospongidae. *f*, Common canal or paragastric cavity. *g*, Inhalent canal, the axial terminus of which was lined with spicules (canalaria). *h*, External opening of the inhalent canal in the cover of the cups. *i*, Marginal elongate external spicules on the periphery of the cups (prostalia pleuralia?). *j*, The hypothetical prostalia marginalia shown on branch II of the reconstruction, text fig. 8. These may have encircled the osculum, as they did in most Paleozoic glass sponges. *k*, Position of the hypothetical paragastric pores. Drawing by Anneliese S. Caster.

Dimensions: Proportional relations are illustrated by text figures 2 and 8, and actual dimensions by photographs on plates 1 and 2. There is no basis for judging actual size of the colony in any respect. None of the branches terminate on the holotype, so all lengths given are incomplete. Over-all length of the axis of the holotype fragment, 300 mm; branch I on the holotype is approximately 150 mm long not following curvature; branch II is about 30 mm long; branch III extends for about 240 mm to the edge of the slab; branch IV runs for 210 mm and branch V for about 200 mm. The diameter of the colony shows uniform variation throughout the colony; the greatest diameter of the cups varies between 12 and 16 mm; the average diameter is about 14 mm; the length of the individual cups varies a great deal, from as little as 4 mm to over 12 mm; the average length, if one is safe in making such an approximation, is about 7 mm. External semireticulum with meres measuring about 0.5 mm to a side;

this is essentially the size of the other nets. Internal dimensions: inner filling usually from 0.5 to 1 mm less in diameter than external mold; the greatest discordance at cup angles; paragastric tube varies from about 4 to 5 mm in diameter, the expanded part usually not being at most more than 2 mm greater in diameter than the rest of the tube. This may be a slightly exaggerated dimension, for the tube shows almost uniform evidence of slight flattening.

Discussion.—In view of the fact that the writer collected the holotype and associated specimens and harbored them for seven years in the firm belief that they were an aberrant nodose "worm burrow," and that their true significance did not become clear until he undertook their description for an ichnological paper, it would not be unusual if the casual observer or even field geologist should first think of these curious fossils in terms of "worm trails" or possibly "fucoids." The inevitable first impression, even of paleontological colleagues, has been that of a "trail of some sort." The structures at first impress one as those of a partially filled worm burrow, having only a nodose, irregular shape, as though formed by a marine worm that had more or less periodically excreted pellets of ingested mud, in much the same manner as several modern marine annelids.

When, however, closer scrutiny shows the regular "surface" reticulations, with their various characteristics, the spicular mat of limonite in the intermediate zone between the outer mold and the inner fill, and the inner reticulated tube which is uniformly present, the idea of a "worm" as well as that of a seaweed, or whatever "fucoids" may be, is definitely eliminated. So far as known, reticula of the sort here described are characteristic of siliceous sponges only.

Assignment to the sponges, however, as they are at present subdivided, is fraught with almost as many difficulties as to "fucoids" and "worms." The reticula make necessary the assignment to the Hexactinellida, but neither the order Lyssacina nor Dictyonina will conveniently contain it, for although almost all the affinities of the reticulum appear to be with the lyssacine sponges, the suggestion of a space-lattice dictyonalia in the inner fill would make the assignment to the Dictyonina necessary. I have tended to discount the space-lattice evidence, and have tentatively assigned the fossil to the Lyssacina. In the Lyssacina, where most of our Paleozoic glass sponges fall, the only available group is the family Dictyospongiidae of Hall, wherein it most emphatically will not fit. Hall and Clarke (1898) hit the crux of the current problem by their statement:

> The compound mode of growth is rare among siliceous sponges and there is no satisfactory evidence that in the family Dictyospongidae there was ever a tendency to duplication of the sponge by budding.

Hall and Clarke wrote elsewhere in the same report as follows:

> The siliceous sponges are either thin-walled or thick-walled. In the latter the considerable substance of the cup permits a full development and differentiation of the external, medial and internal parts of the skeleton, while in the thin-walled sponges these different parts are necessarily condensed, and probably abbreviated or only partly developed. The thick-walled siliceous sponges are of not infrequent occurrence in the earlier faunas, but all of the Dictyospongidae and their most closely allied groups possessed a very thin, almost lamellar skeleton, in which a distinction between dermal and gastral surfaces is not always clearly perceptible.

Did not *Titusvillia* differ in more than one fundamental aspect from the dictyosponges, it might be conceivable that the family should be redefined. It is not uncommon to discover new fundamental structural characters in groups that have supposedly been well known for long. Only recently, for example, the Russians have discovered (personal communication, Walter H. Bucher, 1938) colonial Archaeocyathinae, hitherto undreamed of. To be sure, Clarke did cast some doubt on the finality of his family analysis when, in discussing the Mississippian (Keokuk) dictyosponge, *Mastodictya osculata*, he intimated uncertainty as to the meaning of a budlike swelling at the base of the cup fragment of one of the specimens. However, in the absence since 1898 of additional material showing the same structure, it is likely that the Keokuk specimen was merely deformed. In the curious sponge *Ozospongia johnstoni* Clarke (1918) from the Hinsdale sandstone of the Upper Devonian of New York, branching habitus is definitely established for Devonian

sponges. There may be some question if this genus is truly a dictyosponge, but in the absence of evidence of abnormally thick walls, such as *Titusvillia* possesses, there is less basis for segregating it into a separate family, although it probably merits subfamily recognition.

Perhaps the strongest evidence for considering *Titusvillia* as related to the dictyosponges lies in the external similarity to *Ceratodictya*. The duplex nature of some of the early cups (A-1) in our specimen highly suggests this genus. In *Ceratodictya*, also, there is a strange cuplike shape to certain of the "duplex" nodes. The famous "Burton" (or "Aunt Melinda") sponge in the State Museum at Albany, as well as the illustrated specimens in Hall and Clarke's monograph (1898) both show clearly the strong basis for superficial comparison. Clarke's (1918) *Ceratodictya oryx* from the "Chemung group" near Erie, Pennsylvania, is remarkably similar to *Titusvillia*, especially the specimen figured by him on the right hand side of his plate 2, but shows no evidence of colonial growth, more regular duplication of annulations, and less prominent cuplike development of the nodes, as well as apparently no evidence of a thick-walled condition. If only external molds were found, however, this last statement is hardly justified. *Ceratodictya oryx* shows no reversal of the direction of the component nodes or cups and appears to have a much more regular reticulum than *Titusvillia*. Better material may show that *Ceratodictya oryx* is a Devonian form of the Titusvilliidae. *Ceratodictya* is not known to show any tendency toward colonial growth, has a typically thin dictyosponge wall, and is presumably a phylogerontic genus that specialized in giantism. In other words, it is hardly the form in which one would look for an ancestor for *Titusvillia* from a purely philosophical standpoint, although it did live prior to *Titusvillia*. At present we are inclined to think of this similarity of surface ornamentation as homeomorphy, but of considerable significance in pointing the direction of relationship.

It is significant also in searching out relationships that the paragastric net (see text figure 1, *a*, *b*) of the present genus shows the closest structural similarity to the usual dictyosponge reticulum of any of the spicular elements preserved. Hall and Clarke were satisfied that the usual net of their sponges was of paragastric origin. The thick wall of *Titusvillia* is unique and is utterly unapproached by any known dictyosponge.

One of the most striking anomalies in this colonial sponge is the curious reversal of the direction of the individual cups in the upper part of the colony. There is no doubt of the condition, as the photographs will show. The drawing, text figure 8, is not in the least exaggerated. Were not the inner filling and the paragastric tube as well as the external mold perfectly continuous at the abrupt change, one might conclude that we were dealing with parts of two colonies. The regularity of the branching and the orientation of the component cups as well as the position of the arms also preclude this possibility. A possible, but by no means final, interpretation is that the colony grew upright from the ocean floor with its axis and branches directed upward so long as the relatively strong skeletal mat would support it in this position, but that eventually a point was reached when part of the colony lopped over (at the A-2 and A-3 junction) and thereafter grew in a dependent or even possibly recumbent manner. In the reconstruction to illustrate this view, shown in text figure 3, enough additional upright axis and branches are added below the holotype fragment to make possible the necessary droop of the long distal arms on our specimen, which is represented in the figure by the part above the dotted arc. It is not impossible that some of the arms may have become recumbent, creeping branches eventually, but no evidence of this is shown in the specimens at hand. It seems significant that the strongest vertical bands of spicules on the constricted necks of the cups are in the sections of the axis that appear to have been upright in position. To the writer there is no difficulty involved in visualizing the abrupt change in direction of the individual cups as soon as branches reversed their direction. Such environmentally induced changes in form are the rule in this highly polytrope phylum.

Several of the cups show a tendency for both upper and lower expansions to develop, or for neither to develop completely, as

though there were a conflict of tendencies, such as one might expect if cups are to be formed at ease with their major expansion in an upward direction, depending on the orientation of the colony. Whether there was subsequent readjustment to conform to the gradual change of direction of the arms as more cups were added is uncertain. That the cups with this apparent dual tendency are not especially well developed at the crucial initial parts of the axis or branches might tend to support this last idea.

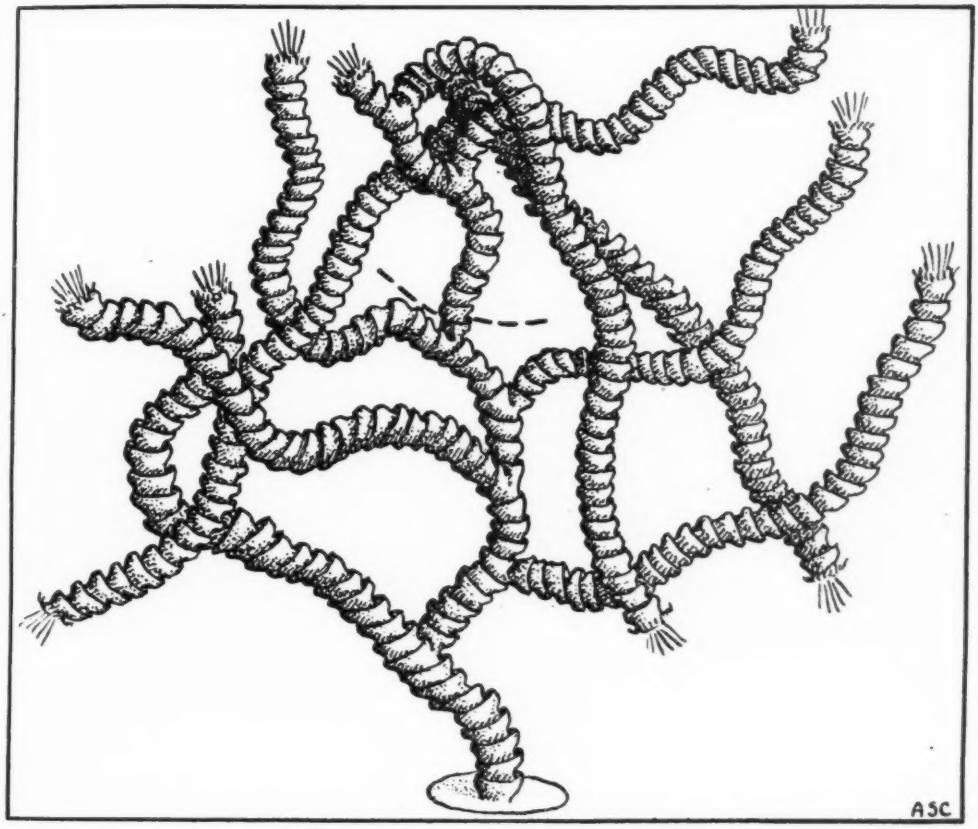

FIG. 3.—An idealized reconstruction of the colony of *Titusvillia drakei* as it may have lived with basiemphytic attachment to the sandy floor of the Mississippian sea, and upwardly directed branches and axis in the earlier part of the colony but with dependant and recumbent branches and axis in the higher parts, where the spicular skeleton would no longer support upright growth. This explanation is offered to explain the anamalous reversed direction of the cups on the more distal portions of the colony. The part below the dotted arc is hypothetical; the remainder of the reconstruction is taken accurately from the holotype. Drawing by Anneliese S. Caster.

The name *Titusvillia drakei* is given in recognition of the place of discovery of the holotype specimen and for the founder of the oil industry in Pennsylvania, without the ramifications of whose enterprise geology and paleontology could not have reached the station of eminence they hold to-day. The "old Drake well" is located on the outskirts of Titusville, and many of the relics of the early days of the industry are preserved in the Oil Museum outside the village.

Occurrence.—The holotype specimen was found by the writer during the summer of 1931 opposite the Titusville Public School

in the floor of Church Run within the village of Titusville, Pennsylvania. The specimen came from the Tidioute member of the Cussewago stage of the Oil Lake series (Mississippian), and was lying along the bedding planes of a light-buff sandstone, which carries a sparse marine fauna. Very indefinite specimens of the same general nodose type have been found at the same horizon on Dennis Run, near Tidioute, Pennsylvania, and scattered through rubble derived from the same member on "Yankee Bush" hill north of Warren, Pennsylvania, associated, in each of the latter places, with an extraordinarily rich marine fauna now in course of description. Similar fragments have also been found in the Hayfield shale in the vicinity of Pleasantville, and Titusville, and in the Kushequa shale and sandstone (Knapp suite) at Kushequa, Pennsylvania, on Kinzua Creek, and from a local sandy layer in the Knapp suite at Johnsonburg, Pennsylvania. (See Caster, 1935, for stratigraphy). It is problematical if the Knapp specimens are conspecific with the present species.

Type.—Holotype no. 22130 in the University of Cincinnati Museum; supplementary material, outlined above, on deposit at the Paleontological Research Institution, Ithaca, New York.

Family DICTYOSPONGIIDAE Hall
Subfamily CALATHOSPONGIINAE Hall and Clarke
CALATHOSPONGIA TIDIOUTENSIS Caster, n. sp.
Plate 3, figures 1, 2

Sponge large, nearly circular in cross-section; base broad, apparently subequal to the aperture in diameter; greatest diameter just above basal attachment where the cup is much expanded, like the base of a Victorian bud-vase. The base appears to have borne broad swellings or bosses, which give a scalloped circumference to the cross section at this zone; the cup was apparently relatively short and squat, if the present specimen is representative. On the holotype fragment the central zone is much constricted immediately above the expanded basal zone, and gradually expanded toward the aperture (possibly mesial bulge of a much larger cup) which seems to attain the expansion of the base. Surface smooth with well-developed reticular pattern imprinted. No suggestion of prismatic faces on the specimen.

Reticulum prominent; composed of primary quadrules which measure 7 mm on a side on the upper surface of the expanded base, and about 11 mm high by 8 mm wide on the constricted neck of the cup; horizontal and vertical fascicles appear to be of equal development throughout. The primary quadrules are subdivided very distinctly by four subsidiary sets of spicules arranged in bands, and evidence is present on the least worn surfaces of a still finer set of reticulations, making six sets of spicular bands for the reticulum. There is no indication of nodes or tufts of external spicules at any of the reticular intersections. On the primary bands there is the usual slight variation in diameter due to occasional crowding of spicular elements, which on enlargement tends to give the surface a woven, crashlike effect. An enlargement of the spicular detail is shown by figure 1, plate 3.

Dimensions: Illustration shown on plate 3, figure 2 is natural size. The height of the incomplete fragment of the holotype about 70 mm; diameter of basal expansion, restored, about 130 mm; diameter of mesial constriction 50 mm; diameter of aperture estimated at about 100 mm and also for the basal attachment; restored height estimated at about 90 to 100 mm.

Discussion.—The genus *Calathospongia* appears to be restricted to the Mississippian. Formerly described species have been derived from the Waverly and Kinderhook only. Of the described species (*C. redfieldi*, *C. carceralis*, *C. carlli*, *C. tiffanyi* and *C? sacculus*) *C. redfieldi*, the genotype, bears the closest resemblance to the present species. *C. redfieldi* is not uncommon in the Waverlyan of Ohio and Pennsylvania. All the species are very similar in gross proportions, but differ in reticular detail. They can be considered similar in proportion only on the assumption that Hall and Clarke were mistaken in thinking the mesial bulge of their holotype was a compressional phenomenon. If the bulge, which shows no signs of being a deformational result, were present in life, as in almost every subse-

quently discovered specimen, then the likeness between *C. redfieldi* and *C. tidioutensis* rests on the assumption that the upward expansion of the latter is really mesial and not apertural. This would satisfactorily explain the curiously squat shape of *C. tidioutensis*. The justification for this view is seen by comparing the present specimen with Hall and Clarke's plate 48, figures 1 and 2, where the same basal expansion with nodose swellings and constricted basal attachment are shown. It appears now, judging from the genotype and subsequently described species, that there are really two form tendencies here included that merit segregation as much as the other dictyosponge form genera, namely, (1) those that have the characteristic form of the genotype, with constricted basal attachment, expanded broadly nodose basal zone, constricted lower neck and broad mesial bulge followed by an upper constricted neck and expanded aperture; and (2) essentially all of the other species attributed to the form genus in which the hourglass shape apparently prevails, i.e., those species with a broadly expanded basal attachment, constricted mesial part and broadly expanded aperture of about the same diameter as the base. *C. tidioutensis* belongs apparently in the more exclusive company of the genotype, and to the form genus by strictest definition. The absence of any evidence of prismatic faces in the present species may also be explained by this comparison, since the genotype shows such evidence only subapperturally.

C. carlli from the Mississippian near Pleasantville, Pennsylvania, the type locality of *C. tidioutensis*, differs from it as well as from the genotype by a much narrower mesial constriction and by reticular detail. *C. tiffanyi* is a much stouter form, with a very rapid apertural expansion, and shares detailed structure with *C. carceralis*, which is far too prismatic throughout to be confused with the present species.

In detailed structural features, on which considerable reliance must be placed when differentiating genera and species in these fossils of so few tangible characters and of such polytrope development, *C. tidioutensis* is comparatively easily differentiated. *C. redfieldi* has much finer reticulations and markedly fewer subdivisions of the primary quadrules. In *C. redfieldi* the primary quadrules are from 3 to 4 mm on a side and the horizontal bands are much stronger than the vertical throughout the cup. In fact, the usual aspect of *C. redfieldi* is that of a horizontally banded cup, the vertical striae being often absent or very obscure. In *C. carlli* the horizontal bands are likewise more strongly developed. In *C. carlli*, however, all traces of prismatic faces are lacking, as in *C. tidioutensis*, on the known parts of the cup. In *C. tiffanyi* the primary quadrules measure on an average 10 by 12 mm, which is considerably coarser than in the present species; furthermore, in the former the primary intersections are obscurely nodose. *C. carceralis* recalls the present form in the prominence of the horizontal and vertical parts of the quadrules, but here again there is disparity, the longitudinal bands being stronger than the horizontal. In *C. carceralis* the quadrules are on an average 8 mm wide by 12 mm high, and the horizontal component is highly variable.

Imprinted on the mold of *C. tidioutensis*, as shown on plate 3, figures 1 and 2, is the mold of a brittle star, which seems clearly to have been inside the basket of the sponge when buried. Although the existence of an oscular sieve plate in the Paleozoic glass sponges is still an open question, the possibility of an entrapped star is raised. Such symbiotic relationships are commonplace in the modern Venus's flower-basket, *Euplectella*, where crabs and other organisms are reported to enter the paragastric cavity when tiny and find they cannot escape later on when growth renders them too large to get through the oscular sieve. That the present star was in the net seems clear. The orientation of the arms and the dissociation of only one arm, and that intact and apparently grasping the reticulum, suggest a trapped organism. This may have occurred after death, to be sure, the skeleton acting in this case like a glass lobster pot or trap on the sea floor.

The star is not well enough preserved to make analysis readily possible, and it is hardly necessary for this paper. It appears, however, on the basis of the presence of single columns of abactinal radial plates (i.e., "vertebrae") to belong with the true

ophiuroids rather than the more common auluroids. If this is the case, the genus is probably new to science. Especially is this true if the termini of the arms are bifid in the basket-star manner, as the mold seems to indicate.

Occurrence.—This species is known from the Tidioute shale and sandstone of the Cussewago stage of the Oil Lake series (Mississippian) in western Pennsylvania. The holotype comes from the Nelson farm, 3 miles N. 50° W. of Pleasantville, where it was collected by J. F. Carll during his work on the Second Pennsylvania Geological Survey. Additional fragments attributed to this species have been found by the writer in the Pleasantville-Titusville area and also at the same horizon on Dennis Run at Tidioute and in the Warren area. It is associated with *C. carlli* and the usually abundant marine fauna of the Tidioute member.

Type.—Holotype no. 3314 in the catalogue of the Second Pennsylvania Geological Survey (Chas. E. Hall, 1878, vol. 0, p. 148) where it is listed as "*Dictyophyton.*" This collection is now on deposit at the Academy of Natural Sciences of Philadelphia. Through the courtesy of Mr. C. M. B. Cadwalader, the Director, the specimen was lent the writer for study. Additional specimens, all less complete than

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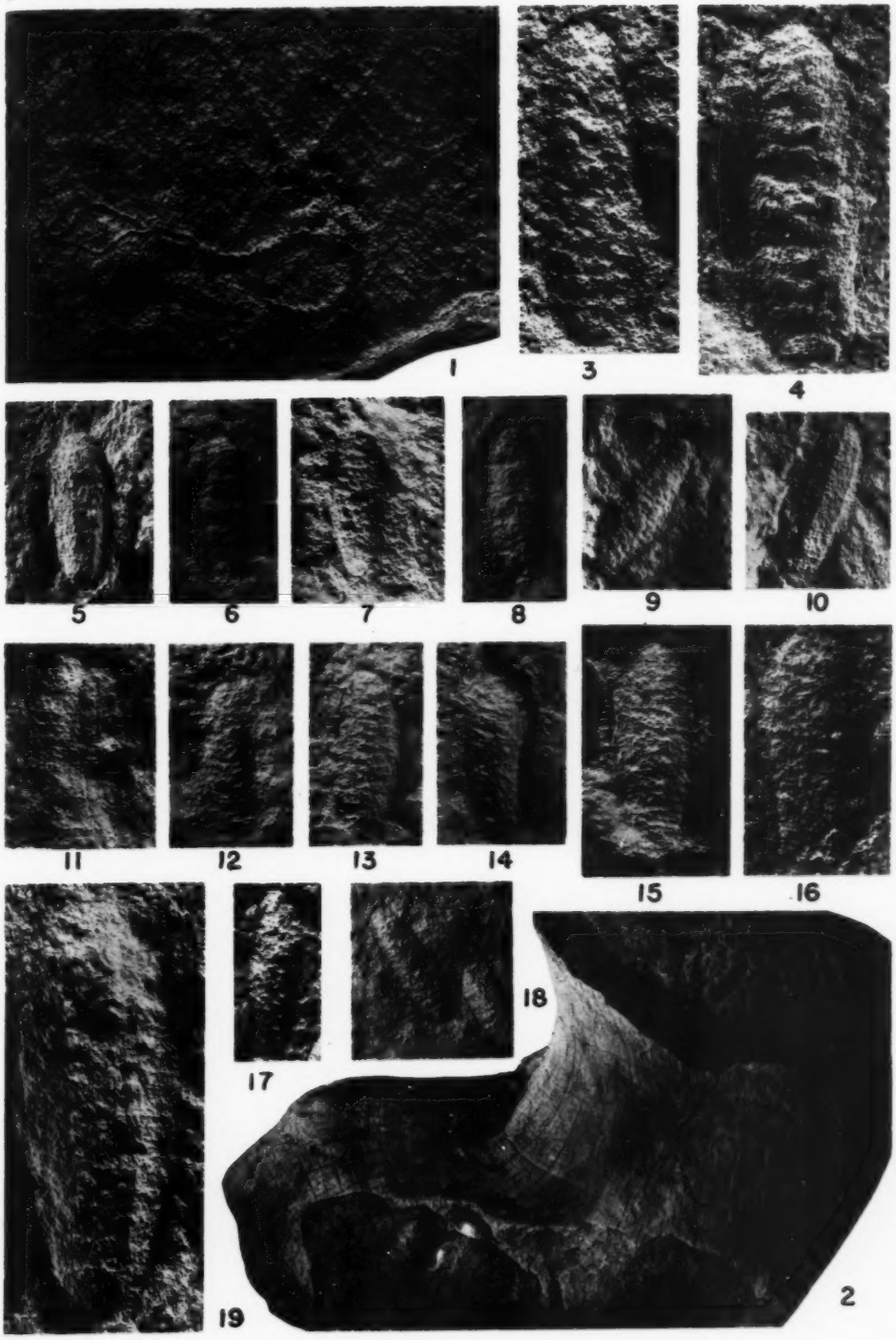
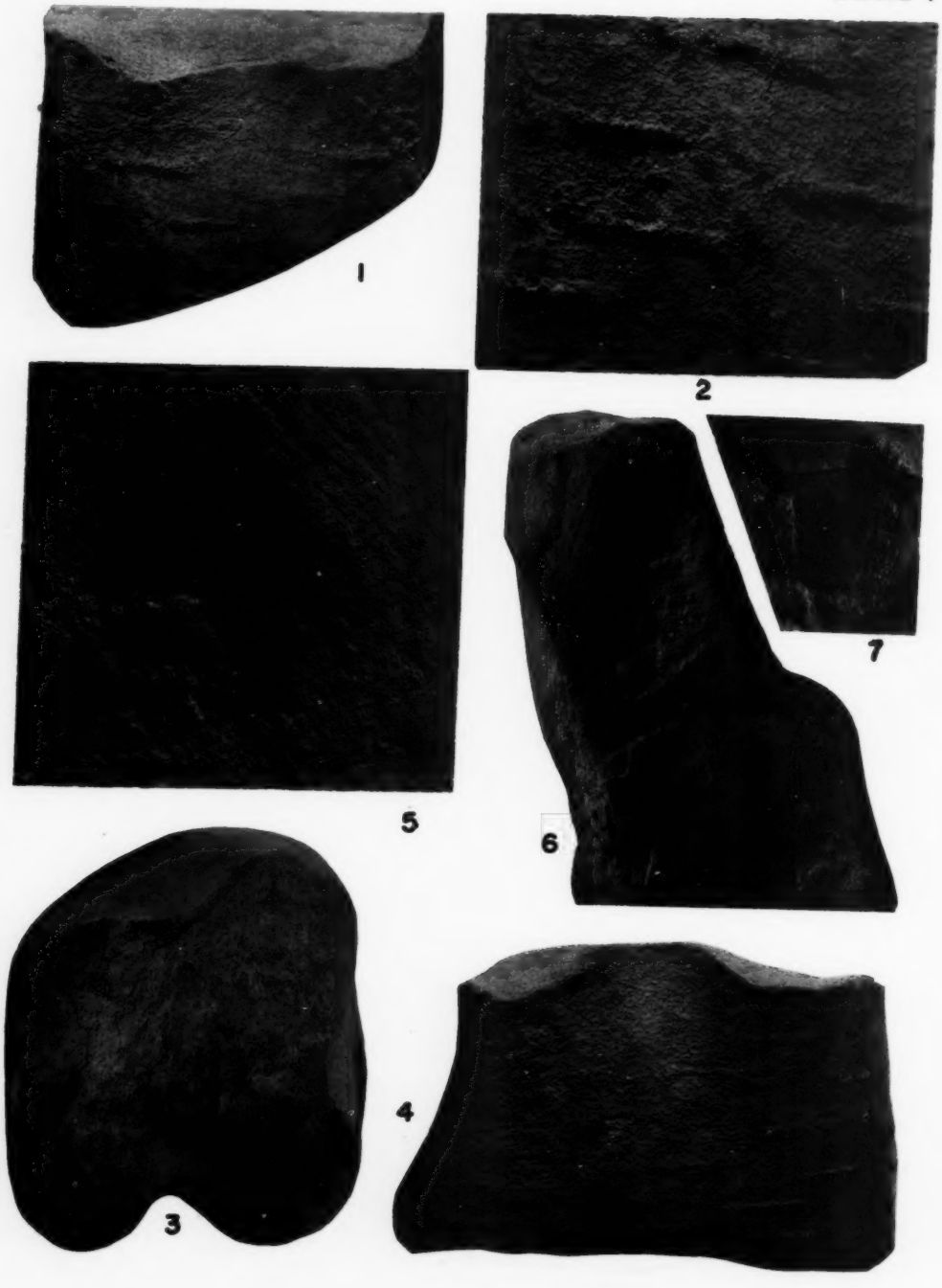
EXPLANATION OF PLATE 3

FIGS. *1, 2*—*Calathospongia tidioutensis* Caster, n. sp. *1*, Englargement of the surface to show the primary quadrules and secondary spicular elements, as well as details of the imprisoned ophiuroid, presumably a new genus, which is impressed on the internal mold of the holotype. It appears that all of the ophiuroid arms may be terminally bifid in the manner of the one so well shown in the lower left. Holotype, no. 3314, catalogue of the Second Pennsylvania Geological Survey, on deposit at the Academy of Natural Sciences of Philadelphia. ×3. *2*, View of the holotype showing the known proportions, the nodose basal expansion, constricted base, and expanded apertural end, or possibly mesial expansion as discussed in the text. Reticulum proportions, general relationships, and position of the imprint of the ophiuroid are well shown. Holotype, ×1. (p. 10)

3–19—*Ithacadictya cornelli* Caster, n. gen., n. sp. *3*, Typical nodular appearance of the internal mold in average specimens where the secondary and even part of the primary reticulum have disintegrated during fossilization. University of Cincinnati Museum no. 22134. Paratype, ×2½. *4*, Shows the usual nodose condition and makes clear why for years these sponges have been considered as "mud balls" in the sandstone; here the transverse strands apparently held for a longer time than the vertical, thus creating the curious constrictions which so many of the specimens show. This is an enlargement of *6*. U.C.M. no. 22133. Paratype, ×2.5. *5*, Prismatic individual on which the primary reticulum and traces of the secondary meres show rather well; the prismodictyan affinities are rather obvious in forms as well preserved as this. U.C.M. no. 2213^. Paratype, ×1. *6*, See *4*, above. *7*, Average individual showing the granular surface aspect which is so commonly observed in the topotypical material; the horizontal elements of the reticulum show well here; note also the the finer grain of the filling than of the matrix material. U. C.M. no. 22135. Paratype, ×1. *8*, A subprismatic individual in which several of the vertical fascicles of the primary net stand out very strongly; this is exceptional for the genus and species. U.C.M. no. 22136. Paratype, ×1. *9*, Curious fusiform individual, which is apparently not deformed by pressure; the pedunculate portion appears to be basad; the surface nodes are highly typical of the usual run of the paratypes. U.C.M. no. 22137. Paratype, ×1. *10*, Prominently prismatic individual, which shows portions of four faces and the curious, but typical cordate nature of the elevated, rounded prismatic angles, and possibly slight tendency for nodes to be formed at the junction of the transverse bands of the primary quadrules and the prismatic angles; seats of spicular tufts at these junctions also suggested here as on *5*. U.C.M. no. no. 22131. Holotype, ×1. *11*, Two individuals that show very clearly the strong horizontal fascicles of the reticulum. U.C.M. no. 22138. Paratype, ×1. *12, 13, 14*, Show some of the variation exhibited by the type material, but also the consistency with which horizontal constrictions appear in the poorly preserved material; U.C.M. nos. 22139, 22140, 22141. Paratypes, ×1. *15, 16*, Slightly enlarged additional paratype material to show surface variations, and also showing variations in outline. U.C.M. nos. 22143, 22144. Paratypes, ×2. *17*, Small individual on which suggestions of definite transverse nodes appear. U.C.M. no. 22144. Paratype, ×1. *18*, Two individuals showing fragments of the vertical secondary reticular net and subprismatic faces. U.C.M. no. 22145. Paratype, ×1. *19*, Enlargement of *5*, ×3. All specimens of *Ithacadictya cornelli* here shown come from the lower shale of the Enfield stage of the Senecan series, Upper Devonian in the Hungerford quarry, near Ithaca, New York. (p. 16)



Caster, Paleozoic Sponges



Caster, Paleozoic Sponges

the holotype, are in the collection of the writer at the University of Cincinnati and on deposit at the Paleontological Research Institution, Ithaca, New York.

CALATHOSPONGIA CARCERALIS
Hall and Clarke
Plate 4, figures 5, 6

From the Tidioute shale and sandstone ("Waverly") at Warren, Pennsylvania, comes a specimen appearing quite definitely attributable to *Calathospongia carceralis*, which has been hitherto confined to the Waverlyan series of Ohio and the Keokuk formation of Indiana. The illustrations bring out very clearly the basis for the assignment, plate 4, figure 6, being mounted upside down to conserve space. The broadly expanding disc and extremely strong verticle fascicles of the reticulum, which give the cup a prismatic aspect, are characteristic.

The horizontal elements of the primary quadrules, though somewhat more prominent than in typical *C. carceralis*, do show the same uncertainty and irregularity of that species. Both sets of primary strands are somewhat more strongly developed than in usual representatives, yet the proportion remains the same. The quadrules are subdivided at least four times, and to the fourth degree are very distinct. As in the typical specimens the size of the quadrule varies in different parts of the cup (Hall and Clarke did not record this fact). Quadrules 8 mm wide by 12 mm high is the size originally described. Here the dimensions vary between 10 mm by 11 mm to 10 mm by 12 mm in different zones on the cup.

The illustrated specimen was collected by Charles Beecher at Warren, and is no. 13660 in the Yale Peabody Museum. Beecher's notation for the specimen was "Waverly, Warren, Pa." Several years of detailed work on stratigraphic problems and on the faunas in the Warren area leads the writer to conclude that the specimen came originally from the Tidioute shale of Mississippian ("Waverlyan") age. It was probably collected on "Yankee Bush" hill where F. A. Randall and Beecher concentrated a large part of their collecting energy on the perischoechinoid horizon in the Tidioute member. The illustrated specimen is part of a sponge mat, which is commonplace in local pockets of the Tidioute. The specimen was made available through the kindness of Professor Carl O. Dunbar of Yale University.

Subfamily CORTICOSPONGIINAE
Caster, n. subfam.

Simple, vaselike cup, tapered at base and constricted at aperture; greatest convexity at upper third; aperture lobate in a strikingly gomphoceroid manner; surface of internal mold finely rugose, with horizontal spicular bands quite prominent, and entire

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EXPLANATION OF PLATE 4

FIGS. *1–4*—*Corticospongia bradfordensis* Caster, n. gen., n. sp., from the Lewis Run sandstone member (lens) in the lower part of the Venango stage of the Conewango series of the Upper Devonian at Lewis Run, Pa. The type exposure is in the shale quarry of the Bradford Brick and Tile Company. *1*, Lateral view of the holotype at the narrowest diameter, showing part of the lobate aperture, and the barklike surface markings. University of Cincinnati Museum no. 22147. Holotype. ×1. *2*, Enlargement of the surface of the holotype to bring out the detail of the lenticlelike, fusiform, interwoven bundles of spicules in the horizontal element of the primary reticulum. Secondary horizontal elements also show in this picture; the lighting is not proper for showing the fine vertical strands. ×3. *3*, Apertural view of the holotype, which shows the quadrilobate nature of the aperture and apertural constriction. ×1. *4*, Side view of the holotype showing the maximum diameter and bringing out, when compared with *1*, the asymmetry of the species. This shows also the corticular nature of the surface pattern, and the invaginations and lobes of the wall as the aperture is approached. ×1. (p. 14)

5, 6—*Calathosopongia carceralis* Hall and Clarke. From the Tidioute shale and sandstone ("Waverly") at Warren, Pa., presumably from "Yankee Bush" Hill, just north of the city. Collected by Charles Beecher. Yale Peabody Museum no. 13660. ×3. *5*, Enlargement, ×3, bringing out the reticular basis for the specific assignment. *6*, Same specimen, ×1. (p. 13)

7—*Titusvillia drakei* Caster, n.sp. Detail of the spicular mat and some of the surface markings of the outer mold at the terminus of branch V on the holotype. The outline of the two cups involved is shown by accentuated line. ×2. (p. 1)

specimen given a barklike appearance by the presence of prominent spicular fusiform swellings in the horizontal fascicles, which in appearance and sporadic distribution recall the lenticle pores of certain woody plants; vertical spicular elements present, but much reduced.

CORTICOSPONGIA Caster, n. gen.

An aberrant genus of dictyosponges having the characters of the subfamily as outlined above; aperture quadrilobate; cup asymmetrical; rectangular in cross-section immediately below aperture; reticulum irregular and incomplete; quadrules obscure; meres likewise; horizontal fascicular elements very much stronger than vertical; vertical rays not fasiculate; suggestion of scattered hexactins over surface in addition to reticulum.

Genotype, *Corticospongia bradfordensis* Caster, n. sp.

CORTICOSPONGIA BRADFORDENSIS
Caster, n. sp.
Plate 4, figures 1–4; text figures 4, 5

Thin-walled hexactinellid sponge of slightly asymmetrical, vaselike proportions; narrow, tapering base; cup radially expands upward for about two-thirds of the height, where the maximum diameter is reached; upper third is gradually contracted and broadly fluted by four upwardly increasing concavities and alternate convexities; the concavities are aperturally extended as rounded flaps or lobes, which are directed inwardly toward the axis of the cup; the intervening convexities, though also constricted, are subaperturally directed outwardly to produce slight lips or flanges, which form broadly excavate apertural saddles; in the middle of each saddle a broad shallow sulcus is developed as the periphery of the osculum is neared, where it is slightly extended as a low mesial lobe. These characteristics are shown by plate 4, figure 4, and by text figure 4. At the zone just above the maximum expansion of the cup, where the submarginal constriction and oscular invaginations first appear, the cross-section of the cup is distinctly quadrangular, as shown by plate 4, figure 3. The asymmetry of the cup is brought out by plate 4, figures 1 and 4.

The skeletal elements preserved in the internal mold consist of an incomplete major reticulum and parts of subdivisions that make partial meres; everywhere the reticulation is obscure, but the primary horizontal components are very prominently developed and show sporadic fusiform swellings made up of enlarged bundles of spicules, which are compactly interwoven by vertical elements and secondary spicular material. The surface aspect of these bundles on the mold is a rugosity that is very similar to the lenticular elevations in many kinds of plants, e.g., cherry or birch, in which prominent lenticle (respiratory) pores are developed. The details of the surface skeleton are shown by text figure 5. Everywhere over the surface in addition to the coarse nodular horizontal bands there are vertical elements that are not arranged into strands or bundles of fibers. These vertical spicular radii are much finer than the horizontal and often are arranged in series diagonal to the horizontal lines or even in irregular arcs, which in places recalls a tapestrylike weave.

The major partial quadrules are thought of as made up of hexacts in which the axis normal to the surface is completely reduced, and in which the vertical surface axis is likewise much reduced, so that the proportion to the horizontal axis is less than 1 to 5. This is shown by text figure 5, *b*. The secondary spicules are possibly more normal reticular hexacts but again show a tendency for the horizontal elements to be the stronger. The woven effect of the swollen bundles is highly characteristic, as is the all-over fine ribbing in tapestry pattern of the vertical rays. Some of the nodes show evidence of the possible presence in life of external dermalia tufts protruding from these points. The spicular elements are too variable to make measurements significant. All of the photographs are natural size.

Discussion.—The constricted lobate aperture and curious nodose reticulum are the characters that set this sponge aside as unique. The general proportions of the cup conform rather closely to vaselike cups of several of the commoner genera of dictyosponges. *Hydriodictya calyx* of the Chemung stage at Naples, New York, is a good example of this generalized vase form, with a constricted apertural region as well. The

apertural fluting is unknown in other forms, however, although some vaselike forms do show irregularities of the reticulum near the aperture.

There is nothing about the original specimen to suggest crushing or deformation of any sort during fossilization. It was found, as a matter of fact, in an upright position in the red sandstone in the midst of an abundant fauna, all elements in which show peculiarities of one sort or another, chiefly giantism (Caster, 1935).

The reconstruction shown as text figure 4 is based on the holotype and one additional fragment presumably also from the holotype specimen. These are the only fragments known despite several weeks of intermittent effort by the writer in the quarry at the type locality, and the constant cooperation of about fifty laborers and their foremen who were exploiting the sandstone layer for road metal during most of one summer. The writer has returned to the quarry many times subsequently by himself and with dozens of students, and although over a ton of prepared fossil specimens have been shipped by him from this locality, not another fragment of the sponge was turned up. This gives the picture of its rarity. The sandstone layer is a waste product in the shale quarry and hundreds of tons of the material had been discarded over the years in an old working; it was this material which the State of Pennsylvania used for road building. This will therefore explain the rare opportunity for fossil collecting in what otherwise would have been a very difficult place. The general faunal relations of this locality have been discussed by Caster (1935) and by Flower and Caster (1935).

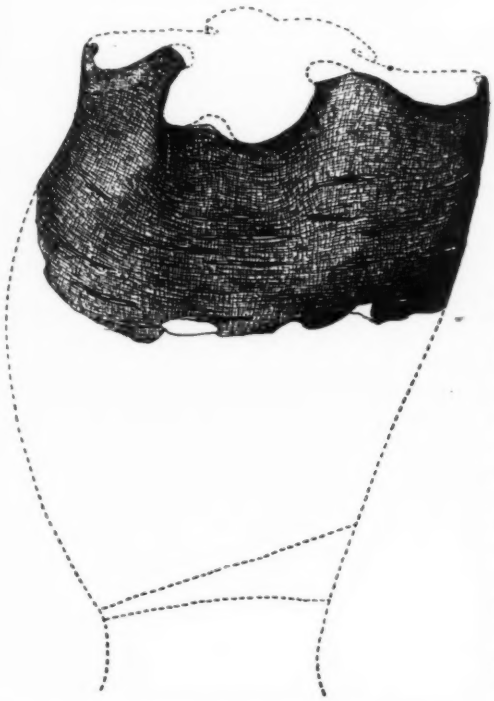

FIG. 4.—Reconstruction of *Corticospongia bradfordensis* based on the holotype and one additional fragment, presumably also from the holotype specimen. The outlines of the holotype fragment are shown in solid line; remainder is hypothetical. The position of the additional fragment, which gave the basis for the shape of the cup here shown, is dotted near the base. There were presumably tufts of dermal spicules in life protruding from the fusiform expansions of the primary reticulum. Surface pattern generalized. Drawing by Anneliese S. Caster.

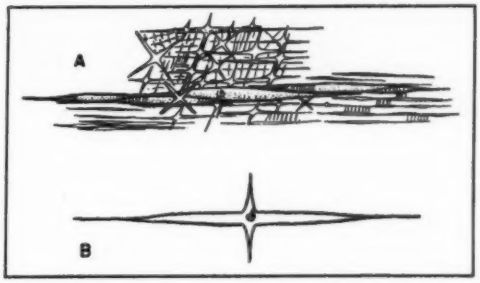

FIG. 5.—Generalized diagram of the spicular detail of the incomplete surface reticulation of the holotype mold of *Corticospongia bradfordensis*. *A*, A composite surface adjacent to one of the lenticlelike nodes of the reticulum, which brings out the prominence of the horizontal elements in the net, the locally crowded zones of single vertical spicular strands, which have been likened to a tapestry weave in textiles; the diagonal orientation of some of the surface hexacts is also shown. *B*, An idealized sketch of a nodular hexact in which the horizontal surface axis is very strong, the vertical element much reduced, and the axis normal to the surface virtually absent. Such spicules seem to be present as the major constituent in the swollen nodes of this species.

Irregularities of the bands constituting

the primary quadrules are not uncommon in the dictyosponges, but the fusiform interwoven bundles in *Corticospongia* appear to be a new development. Nodes that might be compared with the lenticlelike growths on the present species are universally small sacs of the reticulum in other sponges of the Embayment. In none are the nodes or sacs arranged in this horizontal manner in conjunction with definite spicular bands. The generic name, meaning "bark sponge," seems appropriate.

Occurrence.—Corticospongia bradfordensis is known only from the Lewis Run sandstone (Caster and Flower, 1935) member (or lens) in the lower part of the Venango stage (Conewango series) of the Upper Devonian in the brick shale quarry of the Bradford Brick and Tile Co. at Lewis Run, Pennsylvania, about 10 miles south of Bradford.

Type.—Holotype no. 22147, University of Cincinnati Museum.

Subfamily DICTYOSPONGIINAE
Hall and Clarke
ITHACADICTYA Caster, n. gen.

Small elongate prismatic sponge slightly expanded mesially and tapered at both ends; the basal terminus is more acute and more gradually contracted than the oscular terminus; eight prismatic faces which show a tendency to disappear on many individuals; surface nodose in many individuals, probably due to compaction; reticulum consists of regular subequal-sided quadrules, which are subordinately divided into meres to about the fourth degree; skeletal strands very weak, often tending to disintegrate on fossilization; horizontal bands of primary series usually a little more prominent; spicular tufts were present in life at the intersections of the horizontal primary bands and the prismatic angles; the diminutive size of this prismodictyan is perhaps its most characteristic feature.

Genotype, *Ithacadictya cornelli* Caster, n. sp.

ITHACADICTYA CORNELLI
Caster, n. sp.
Plate 3, figures 3–19, text figure 6

Sponge small, stubbedly cigar-shaped, prismatic, with eight essentially flat faces; basal end narrower and more gently tapering than oscular end; prism angles slightly produced on the holotype as low rounded ribs or corrugations; prismatic faces smooth in well-preserved specimens but in others uniformly nodose, due presumably to the breaking down of the secondary reticular elements and the squeezing through the net of the internal fill during compaction; the fraility of the net seems to be a consistent specific character. The primary reticulum on exceptionally well preserved individuals consists of quadrules that are apparently as wide as the prismatic faces and vary similarly in size; the height of the quadrules is apparently consistently equal to the width. The secondary reticular net, when preserved, regularly subdivides the quadrules to the fourth degree; all specimens show a tendency for the horizontal spicular bands to be much more strongly developed than the vertical, thus giving the impression of horizontal constrictions on the inner fill of the partly disintegrated forms. A reconstructed specimen and spicular details are shown on text figure 6.

Dimensions: The photographs on plate 3 are natural size unless otherwise indicated. The length of the sponges varies from 20 to 24 mm and the diameter is usually between

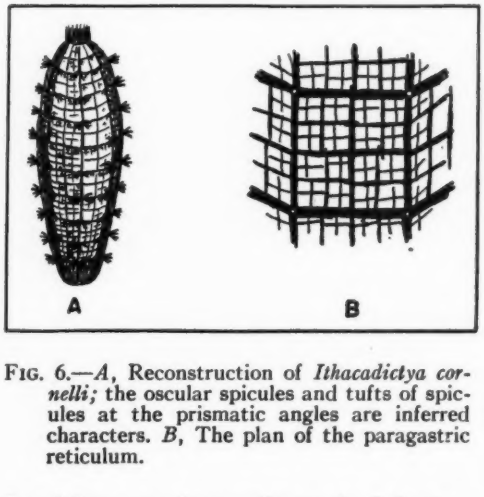

FIG. 6.—*A*, Reconstruction of *Ithacadictya cornelli;* the oscular spicules and tufts of spicules at the prismatic angles are inferred characters. *B*, The plan of the paragastric reticulum.

5 and 8 mm maximum. So much of the material has been deformed in compaction that measurements of most specimens can mean very little. The holotype is 25 mm

long and has a maximum diameter of 8 mm, a basal terminus of 4 mm and an oscular diameter of 3 mm. A well preserved paratype measures 21 mm in length and 4 mm in diameter at the osculum and 3 mm at the base; maximum diameter 8 mm.

Discussion.—For years these diminutive sponges have been quarried by the tens of thousands in the Hungerford and University quarries near Ithaca, New York, in the fine sandstone used as the modern building stone of Cornell University (the stone formerly used is a local coquinite). The sponges occur as tiny mud pellets usually in the midst of the sandstone, or as finer sandstone nodes along the planes at which the dense layer (2–3 feet) will easily split. They have been passed by for years as "mud balls" or other "sedimentary" phenomena characteristic of the magnafacies (Smethport) in the Embayment just seaward of the red facies (see text figure 7). The justification for this casual interpretation is easily seen by looking at the pictures of imperfect sponges on plate 3. Such individuals occur by the hundred for every one that shows recognizable shape and markings. In all only about a dozen individuals out of many hundred examined are known to show the surface reticulation and prismatic angles clearly.

The associated fauna comprises among other forms, *Eutaxocrinus ithacense*, which is locally quite abundant; *Spirifer mesistrialis*, which is likewise common in zones; "*Spirifer mesicostalis*," which is not common; *Productella speciosa*, *Lepidechinoides* sp., and great numbers of inarticulate brachipods, among which is an undescribed *Lingula* and a new genus apparently of orbiculoid. Much triturated gymnosperm wood and a curious flabellar alga are present.

The systematic affinities of the sponge are entirely with the prismodictyan dictyosponges of the overlying Chautauquan series. On the basis of its shape and reticular detail it is looked upon as a diminutive ancestor of the *Prismodictya* line and may be eventually considered as a subgenus in that divisible form genus. *Ithacadictya* represents the only Senecan representative of the stock so far. (Clarke's *Prismodictya palaea* from the "Portage" group in the Naples area is really of Chemung age, as Chadwick's stratigraphic work (1935) has shown.) *Ithacadictya* differs from *Prismodictya*, s. s., in being much smaller than any known form of that genus, in having a comparatively weak secondary reticulum, and a nearly isotelous shape. The small size of *Ithacadictya* is apparently an ephebic character, for never has a larger sponge of any sort been found in the quarry, which covers an area of many acres.

Likewise, the Ithaca sponge differs from all of the described species of *Prismodictya* in size, general proportions and reticular details. To even a casual student of the memoir on Devonian sponges, it is clear that too many species of *Prismodictya* have been described, and that several "stocks" are included in the one genus. Among the cigar-shaped sponges belonging in the genus *Prismodictya*, s.s., the species *P. telum* most closely recalls the present forms in general outline and proportion; *P. telum* is, however, nearly thrice as large, has a larger aperture and apparently no subordinate reticula like those of *I. cornelli*. *P. telum* shows a tendency to develop true nodes on the prismatic angles in the upper third and occasionally, a slight apertural expansion (e.g., Hall and Clarke, 1898, pl. 35, fig. 8). Sometimes it grew spirally (idem, pl. 42, fig. 2). Among the group of species that Hall and Clarke were prone to look upon as small for the genus, most of which were at least as large as *P. telum*, is *P. cithara*. *P. cithara* grew to be on occasion four times as large as *Ithacadicta cornelli* and had a well-defined basal constriction or pedicle as well as elongate nodes on the angles. A curious upper mesial globose expansion of the vase is highly characteristic of it. *P. narthicea*, a small species, is presumably conspecific with *P. cithara*, the characters of which it shares in subdued form. Of about the same size as *P. telum*, *P. cercida* is of mesially expanded fusiform shape, has a very tiny aperture, and bears elongate nodes on the prism angles at the zone of major expansion. *P. amicitiae* is a graceful, cigar-shaped form more than four times as large as *I. cornelli*. Like *P. palaea*, which is about twice the size of *I. cornelli*, it is characterized by having its major convexity in the lower third. None of these small prismodictyans shows a tendency for the horizontal spicular bands

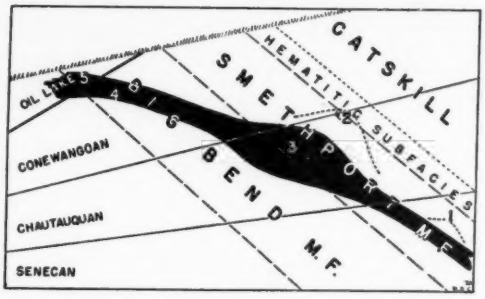

FIG. 7.—Highly generalized facieological distribution chart of the Upper Devonian and lower Mississippian siliceous sponges in the Penn-York Embayment, with special reference to forms discussed in this paper. The large sigmoidal lens shows the major environmental distribution; the dotted line indicates the general limits of the aberrant forms herein described in relation to the axis. To be sure, there were since very ancient times siliceous sponges in considerably more seaward facies than here shown, but during the time here indicated they appear to have been very scarce in the Embayment; at least they are not well known. *1*, Occurrence of *Ithacadictya cornelli* Caster in the near-shore subfacies of the Smethport magnafacies. *2*, The unusual environment of *Corticospongia bradfordensis* in the marine hematitic subfacies of the Catskill magnafacies. *3*, Zone of maximum development of the Dictyospongiidae in the Embayment. *4*, The uppermost Devonian occurrences of dictyosponges in the Warren County area of Pennsylvania. *5*, Western Pennsylvania and eastern Ohio occurrences of siliceous sponges in the "Waverlyan," including *Titusvillia drakei*, *Calathospongia tidioutensis* and *C. carceralis*. Facieology from Caster, 1934, 1938.

to be more prominently developed than the vertical; all appear to show nodose tendencies on the prism angles, and as a matter of fact appear to grade quite imperceptibly into the less nodular representatives of the "genus" *Hydnoceras*, e.g., *H. anthracis*. It is not impossible that the Ithaca sponges are as much related to this last genus as to *Prismodictya*.

Occurrence.—This species is known only from the lower beds in the Enfield stage of the Senecan series (Upper Devonian) near Ithaca, New York. The type locality is the Hungerford quarry on the White Church Road, town of Ithaca, New York, about two miles east of the campus of Cornell University. Specimens also occur at the same horizon in the University quarry a mile farther east along the same hillside (the "Portage escarpment"). The sponges occur only in the more massive greenish-blue relatively pure sandstone layers, which also occasionally contain many reddish mud pellets and a marine fauna. The rock tends to turn pinkish upon weathering.

Types.—Holotype no. 22131 and paratypes 22132–22145, University of Cincinnati Museum. Additional paratypes are in the collection of the writer. There are also some paratypes on deposit at the Paleontological Research Institution, Ithaca, New York. Several large slabs covered by sponges, also paratypes, were left at Cornell University by the writer in 1935.

EXPLANATION OF TEXT FIGURE 8

FIGS. *1*—Reconstruction of *Titusvillia drakei* from impressions taken from the holotype material. Lay-out of the colony and profile of the cups exactly as on the original specimen; surface reticulations very accurately shown, but on the holotype they are preserved on only a little less than one-fourth of the exposed surface, and are often obscure. The prostalia marginalia spicules as shown on branch II are entirely hypothetical, but judging from living and extinct forms of somewhat similar organization, were probably present at the terminus of each branch in life; branch II is definitely an incomplete branch on the holotype. The peripheral ring of pleuralia spicules shown on several of the cups is distinctly indicated in several places on the holotype and should have been shown on each cup undoubtedly. The reversed orientation of the cup in the *A-1* and *A-2* portions of the axis and in branches III, IV and V is as in the holotype, one explanation of which is shown by text figure 3. The *A-1* section of the axis shows duplex annulations, which have been compared to those of *Ceratodictya* of the Dictyospongiidae in seeking for taxonomic relationships. ×$\frac{2}{3}$.

2—Plan sketch of the holotype slab showing the attitude of the entire colony so far as known, and by the rectangle, the part of the holotype shown. ×$\frac{1}{3}$.

3—Longitudinal composite section through parts of a colony of this sponge. This brings out the relations between the external mold, the inner filling, and the paragastric tube. This relationship has been discussed in the text, and is diagrammatically interpreted by text figure 2. ×$\frac{2}{3}$.

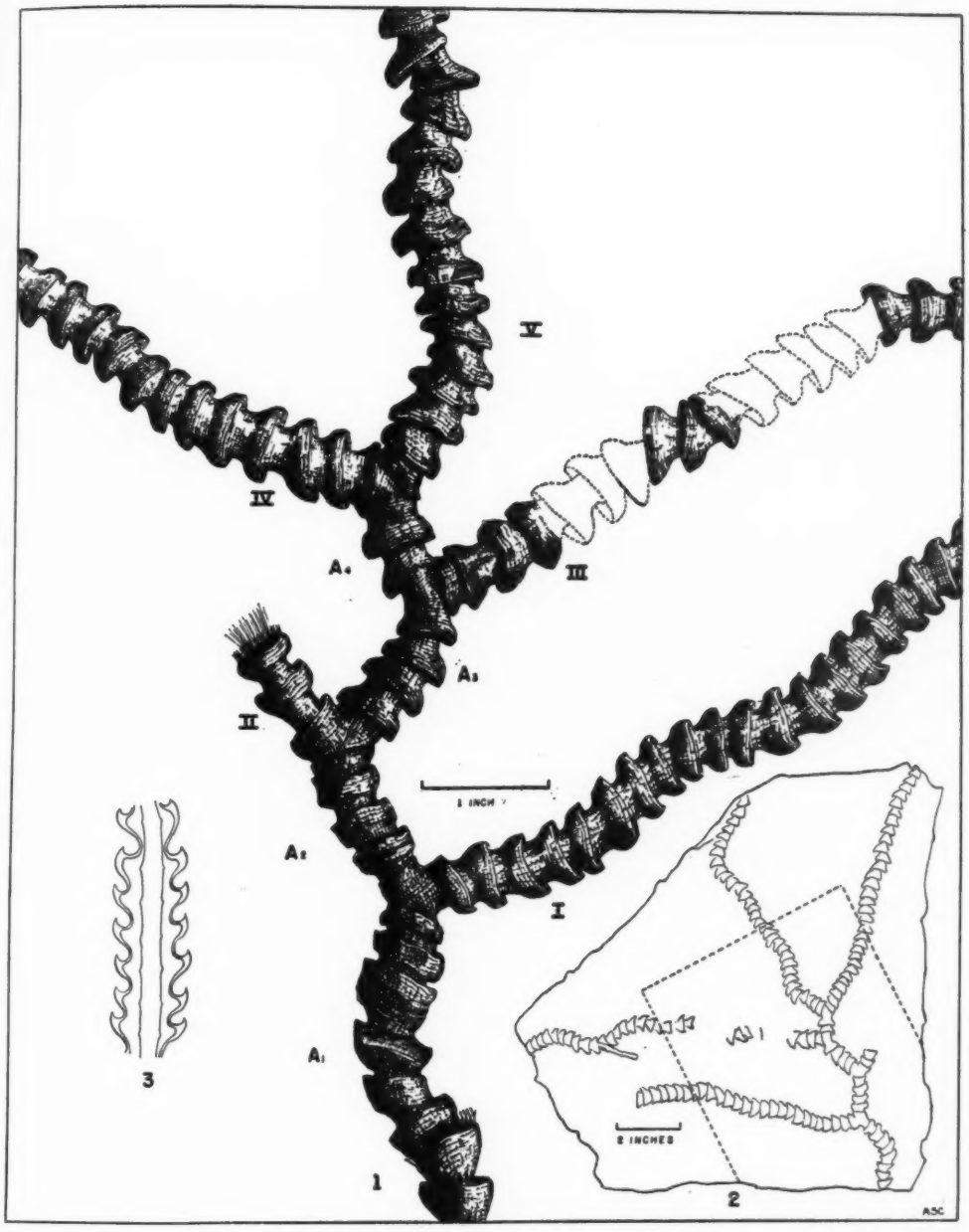

FIG. 8—*Titusvillia drakei* Caster, n. sp. Drawings by Anneliese S. Caster.

SUMMARY OF OCCURRENCE

The new sponges here described lived in essentially the same environment as virtually all of the Upper Devonian dictyosponges heretofore described. The magnafacies zone apparently best suited to them is one of sandstone and shale deposition just slightly seaward of the contact between the Smethport and Big Bend magnafacies. The color of the enclosing sandstone (the preserving medium of dictyosponges is almost invariably sandstone) is usually chocolate to pinkish. It appears that the later sponges, especially the lower Mississippian forms, dwelt near the central subfacies of the Big Bend facies zone, slightly farther out to sea than the Devonian forms, though in a zone still characterized by clastic sediments of considerable coarseness. The *Ithacadictya* lived well within the edge of the Smethport magnafacies, where most of the strata are greenish when freshly exposed but upon weathering tend to become pinkish. This is slightly nearer shore than the average. *Corticospongia* lived nearer shore than any other known dictyosponge. Its environment was a peripheral hematitic subfacies of the Catskill magnafacies, which subfacies, as developed at Lewis Run, carries an abundant marine fauna, most forms of which are aberrant (Caster, 1935). The remainder of the sponges described herein, occurring in the highest Devonian and basal Mississippian strata of the Enbayment, lived in somewhat more seaward subfacies. The life zone of the Warren specimens was the most landward subfacies of the Big Bend magnafacies and the specimens from Pleasantville and Titusville occupied sandstone lenses well within the Big Bend ("typically marine") province. (See Caster, 1934, 1938 for facieology.) Figure 7 brings out the gross distribution of the siliceous sponges in the Embayment during Upper Devonian and Mississippian time and shows the facieological shift seaward of the group as whole, some aspects of which the current paper illustrates.

ACKNOWLEDGMENTS

During the course of this study many colleagues at the University of Cincinnati at large, and in the Department of Geology and Geography, have been of material assistance, especially as "testing ground" for ideas, some of which are not herein incorporated: The Faber Publication Fund for Paleontology at the University of Cincinnati Museum and the Faber endowed curatorship at the Museum have made this study possible. Specimens were loaned for study through the courtesy of Mr. C. M. B. Cadwalader, Managing Director of the Academy of Natural Sciences at Philadelphia and Professor Carl O. Dunbar of Yale University. The credit for the fine photographs goes to my competent undergraduate assistant, Mr. Stewart Jones, and for the line drawings to my wife, Anneliese S. Caster, who merits fullest recognition as joint worker on this research.

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REVISED NOMENCLATURE FOR SOME NUCULID PELECYPODS

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ABSTRACT—This paper discusses 60 names that have been applied to nuculid pelecypods. A partial abstract was published in the Proceedings of the Geological Society of America for 1935 (June, 1936), p. 368, under the title, "Revision of nuculid pelecypods." The following are described as new species: *Nuculopsis okawensis*, *Nuculopsis welleri*, and *Nucula capayensis*. The following are new names: *Nuculopsis croneisi* (for *Nucula parva* McChesney), *Nucula atacellana* (for *N. cancellata* Jeffreys), *Nucula lattorfiana* (for *N. rugulosa* von Koenen), *Nucula marshalli* (for *N. uruguayensis* Marshall), and *Nucula thielei* (for *N. aequalis* Thiele).

DESPITE the abundance of the bivalved mollusks from Ordovician times to the present day, and despite a voluminous literature dealing with them, there still remain wide gaps in our knowledge of the group. Our records of the geologic, geographic, and bathymetric distributions of the bivalves are regrettably incomplete, though the merit of these animals as indicators of substrate, depth, and water temperature has often been recognized. A certain number of accurate records have been made, of course, but too often we have been content to substitute suppositions for actual observations. Even the classification of the group is unsatisfactory, because, at least in part, of differences in the subjective criteria employed by various students. Faulty nomenclature, moreover, plays no small role in obscuring relationships.

So much confusion, indeed, has developed that a conscientious worker often hesitates to identify specimens, knowing he cannot be certain that the biological entities with which he is dealing are properly coordinated with any of the published names which might be available. Coordination, naturally, must be attained if facts, opinions, and conclusions are to be expressed unequivocally —a name must have a precise connotation before it can be used as evidence leading to a correct deduction. For example, if two or three different species carry the same name, erroneous statements regarding geographic and stratigraphic distribution may be made. The problem confronting the taxonomist is basically one of language—the definition of biological entities in unambiguous words. One of the first steps to be taken, then, toward the proper elucidation of any molluscan group is a consideration of its homonyms.

Random renaming of homonyms is not advocated. In a recent paper (16), I made no attempt to apply a new designation to the homonym "*Nuculopsis*" Woodring because lack of specimens made uncertain the validity of the biologic unit under consideration. The present paper does not imply a change of conviction regarding the appropriateness and value of renaming homonyms; instead the following statement by Stewart (20) is endorsed:

> The proposal of substitute names for homonyms without knowledge and designation of the type material is a thing which careful workers do not do . . . There is as much responsibility, if not more, in the proposal of a substitute name as in a new name, therefore those who carelessly scatter substitutes for homonyms should be discouraged.

The significance of the present paper (and of others like it) is that by the attempt to coordinate nomenclatural and biological units the way is cleared not only for a more precise knowledge of distribution but also for a better understanding of the composition of families. This understanding is desirable because, more than any other taxonomic category, the family seems to promise a lead toward a satisfactory grasp of the complex interrelationships of the Pelecypoda. Since many scientific hypotheses and theories—floating continents, migrations, interregional synchronizations of strata, climatic changes, and the like—hinge upon the distribution of fossil and Recent organisms, the degree of accuracy in citation of

these organisms becomes a matter of importance. Large units harbor too many exceptions to be of much utility except for the broadest generalizations; minutely defined small units are, on the other hand, beyond the domain of anyone but the molluscan specialist. At least for the bivalved mollusks, the family category, painstakingly delimited, appears to be a unit of intermediate size that will satisfy most of the demands both of the systematist and of the general scientist. It is hoped that this paper will constitute a step toward an adequate comprehension of the family Nuculidae.

HOMONYMS NOT TREATED

Some of the homonyms not considered in this paper because of insufficient data are the following:

Nucula amica Gardner, 1916, *not* Barrande, 1881?
Nucula cancellata Vredenburg, 1928, *not* Meek and Hayden, 1856.
Nucula cuneata Phillips, 1836, *not* Sowerby, 1833, *not* Koch and Dunker, 1837, *not* Münster, 1841, and others.
Nucula donaciformis Harder, 1913, *not* Hall, 1847, *not* E. A. Smith, 1855.
Nucula elongata Sowerby, 1833, *not* Daudin, 1801, etc.
Nucula impressa Conrad, 1849, *not* Sowerby, 1824, *not* Hall, 1845.
Nucula inflata Wissmann, 1841, *not* Sowerby, 1827.
Nucula lunulata Girty, MS, *in* Morningstar, 1922, *not* Nyst, 1845.
Nucula minima Foerste, 1885, *not* Sowerby, 1818.
Nucula minor Venzo, 1933, *not* Deshayes, 1860.
Nucula minuta Owen, 1839, *not* Fleming, 1813, *not* Defrance, 1825.
Nucula obliqua Say, 1820, *not* Lamarck, 1819, *not* Münster, 1841, *not* Girty, 1909.
Nucula obsoleta McChesney, 1860, *not* Goldfuss, 1837.
Nucula serrata Shumard, 1859, *not* Sowerby, 1850.
Nucula simplex Adams, 1856, *not* Deshayes, 1842.
Nucula striata King, 1832, *not* Lamarck, 1805, *not* Sowerby, 1833.
Nucula tumida Hinds, 1843, *not* Roemer, 1843.
Nucula umbonata Hall, 1883, *not* Seguenza, 1877.
Nucula ventricosa Pčelincev, 1927, *not* Fleming, 1828, *not* Hinds, 1843, *not* Hall and Meek, 1854, *not* Hall, 1858.

ADDITIONS TO NAMES OF SPECIES OF NUCULA

The mechanics of renaming homonyms and the description of new species necessitates the following additions to the list of names that have been used with the generic name *Nucula* (16*a*); the list below also includes other names omitted from the previously published one.

albiplanata
alcocki
ancervillensis
atacellana
bantamensis
barcellonensis
billeborgensis
capayensis
caucasica
croneisi
doris
doucieusi
fenestralis
frencheni
friisi
gadsdenensis
girtyi
hokoensis
kyushuensis
lattorfiana
luciae
marshalli
martini
monumentorum
morundiana
myiformis
ngatutura
nigella
observatoria
obtenta
osawaensis
peelii
perkëo
phayreiana
pietzschi
radiacostata
schlosseri
submucronata
syriaca
tenuicostata
thielei
transsylvanica
tunicata
ungulella
waltonia
whitei
yanagawaensis
zwierzyckii

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The typescript has been improved by the suggestions of D. L. Frizzell, A. Myra Keen, Siemon Wm. Muller, P. W. Reinhart, and W. Egbert Schenck.

NUCULID PELECYPODS

"NUCULA" ILLINOIENSIS
Worthen, 1884
Plate 7, figures 13–16

Nucula illinoiensis WORTHEN, *1884*, Illinois State Mus. Nat. Hist., Bull. 2, p. 15; *1890*, Geol. Survey, vol. 8, p. 128, pl. 19, figs. 4, 4a.

Nucula illinoisensis Worthen. MILLER, *1889*, North Am. Geology and Paleontology, p. 495. —WELLER, *1898*, U. S. Geol. Survey Bull. 153, p. 378.—HERNON, *1935*, Jour. Paleontology, vol. 9, no. 8, p. 690.

Type material.—No. 2519, Worthen collection, Illinois State Museum, Springfield.

Type locality and age.—"Oolitic bed of the St. Louis limestone, Monroe County, Ill." (Probably Ste. Genevieve limestone, according to J. Marvin Weller, letter dated Jan. 4, 1936). Mississippian.

Material examined.—Holotype and cotypes.

Original description and orthography.—The original description of this species was repeated verbatim in the Geological Survey of Illinois, volume 8 (1890), p. 128. The spelling was "*illinoiensis.*" The name labels accompanying the proterotypes have the same spelling.

Proterotypes.—The specimen figured by Worthen, a right valve 10 mm in length and 7.4 mm in height, is the holotype. It is poorly preserved (pl. 7, fig. 16). Figure 15 is a drawing of the specimen. The shell has a distinct angulation between the dorsal margin and the anterior extremity. The nature of the beaks, exact profile, and hinge cannot be determined; the generic and family identification of the holotype is consequently uncertain. Traces of concentric sculpture can be seen under the microscope. General form and sculpture thus suggest that the holotype belongs to the genus *Astartella* rather than to *Nuculopsis.*

The other two proterotypes are also poorly preserved. One is shown in plate 7, figures 13 and 14, a left valve having the following dimensions (in millimeters): length, 10; height, *ca* 7.5. The marked difference in profile between this fossil and the holotype is apparent. The concentric ornamentation is visible, but worn. The interior is not available. The specimen is not conspecific, and probably not congeneric, with the holotype, but is more likely the new species *okawensis.*

NUCULOPSIS (PALAEONUCULA?) OKAWENSIS Schenck, n. sp.
Plate 7, figures 9–12

Holotype.—No. 38599, Walker Museum, University of Chicago; paratype no. 2079, Schenck Collection, Stanford University.

Type locality.—One and one-quarter miles northeast of Ruma, Illinois; lower Okaw limestone, Mississippian (Chester Group); collected by Stuart Weller.

Description.—Shell subquadrate; dorsal margin straight; anterior extremity broadly rounded and not truncate; ventral margin convex; posterior side straight; beaks worn, apparently orthogyrate; concentric ribs wide, straplike; lunule and escutcheon poorly defined; interior not available. Dimensions (in millimeters): length, 7.7; height, 6.3; thickness, 4.5

Comparisons.—*N. okawensis* differs from the typical "*Nucula*" *illinoiensis* Worthen in profile and sculpture. In fact, Worthen's species may belong to a family other than the Nuculidae. "*Nucula*" *levatiforme* Walcott (U. S. Geol. Survey Mon. 8, p. 22, fig. 1) is more trigonal. *N. wewokana* Girty (U. S. Geol. Survey Bull. 544, pl. 13, figs. 6–8) differs in sculpture and profile, as does *N. pulchella* Beede and Rogers (Kansas Univ. Quart. vol. 8, no. 3, pl. 34, figs. 5, a, b, c). Future work may test the possible significance of the fact that *okawensis* is from beds believed to be higher stratigraphically than the formation carrying the holotype of "*Nucula*" *illinoiensis.*

NUCULOPSIS (PALAEONUCULA) WELLERI Schenck, n. sp.
Plate 7, figure 5–8

Holotype.—No. 38958, Walker Museum, University of Chicago; paratype no. 2078, Schenck Coll., Stanford University.

Type locality.—One and one-half miles south of Marigold, Illinois; lower Okaw (Marigold Oolite), Mississippian (Chester Group); collected by Stuart Weller.

Description.—Shell small, subtrigonal; dorsal margin slightly convex upwards, anterior extremity sharply rounded, ventral margin arcuate; posterior side convex outwards, extending beyond angulation running from beaks to ventral margin, beaks appressed, orthogyrate; lunule clearly defined, elongate; escutcheonal region set off by angulation; ornamented by regularly-spaced, straplike, low concentric ribs, which do not pass on to the escutcheonal area; hinge not visible. Dimensions (in millimeters): length, 7.0; height, 4.5; thickness, 3.4.

Comparisons.—This species is related to "*Nucula*" *wewokana* Girty and to *Nuculopsis croneisi* Schenck, but differs from both in shape and ornamentation, the contrast between the latter and *welleri* being brought out by figures 1–4 and 5–8, plate 7. "*Nucula*" *yuani* Chao (Palaeontologia Sinica, ser. B, vol. 9, fasc. 3 (1927) pl. 1, figs. 1, 1a–d) may prove to have affinities but no specimens of the Asiatic species are available for comparison.

NUCULOPSIS? POPOSIENSIS (C. Branson), 1930

Nucula poposiensis C. BRANSON, *1930*, Univ. Missouri Studies, vol. 5, no. 2, p. 42, pl. 10, figs. 1–6.

Holotype.—University of Missouri.

Type locality.—"Pustula member and Lower Phosphate member (?): Wind River Mountains, Wyoming."

Material examined.—Five topotypes (Schenck coll. 2077) from the Phosphoria formation of Big Popo Agie Canyon, Wyoming.

Remarks.—This species is based upon poorly preserved specimens ranging up to about 13 mm in length. The material examined does not permit of a certain allocation to *Nuculopsis;* the hinge, however, appears to be that of a nuculid.

NUCULOPSIS (PALAEONUCULA) CRONEISI Schenck, new name
Plate 7, figures 1–4

Nucula parva MCCHESNEY, *1860*, Description New Pal. Foss., p. 54, (not seen); *1868*, Chicago Acad. Sci. Trans., vol. 1, pt. 1, 1867, pp. 39–40, pl. 2, fig. 8, pl. 7, fig. 5.—MEEK and WORTHEN, *1873*, Illinois Geol. Surv., vol. 5, pt. 2, sec. 5, p. 589.—MEEK, *1876*, U. S. Geol. and Geog. Survey Terr. 9th Ann. Rept., p. 99. —WELLER, *1898*, U. S. Geol. Survey Bull. 153, p. 379.—GIRTY, *1911*, New York Acad. Sci. Ann., vol. 21, p. 131; *1915*, U. S. Geol. Survey Bull. 544, p. 110.—MORNINGSTAR,

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EXPLANATION OF PLATE 5

FIGS. *1, 3, 7, 8*—*Nucula* (*Nucula*) *darella* Dall. Holotype, U. S. National Museum no. 111424, U. S. Bur. Fish. "Albatross" sta. 2923, off San Diego, California, 822 fathoms, ×6. Recent. (p. 26)

2, 6, 11, 15—*Nucula* (*Ennucula?*) *linki* Dall. *11, 15*, Holotype, U. S. Nat. Mus. no. 107649, U. S. Bur. Fish. "Albatross" sta. 3034, off Point Fermin, California, 24 fathoms, ×6; *2, 6*, hypotype, U. S. Nat. Mus. no. 206692, U. S. Bur. Fish. sta. 2860, off Queen Charlotte Sound, British Columbia, 876 fathoms, ×6. Recent. (p. 33)

4, 5, 9, 10, 13, 16—*Nucula* (*Nucula*) *atacellana* Schenck, new name for *Nucula cancellata* Jeffreys. Lectotype, U. S. Nat. Mus. no. 197154; Jeffreys Coll., ×6. Recent; Porcupine Exped. sta. 21, 28, Northwest of Ireland, 1476 and 1215 fathoms. (p. 27)

12, 14, 18, 21—*Nucula* (*Ennucula*) *cardara* Dall. Holotype, U. S. Nat. Mus. no. 265905, ×2½. U. S. Bur. Fish. sta. 5673, 100 miles south-southwest of San Diego, California, 1090 fathoms. Recent. (p. 34)

17, 19, 20, 22—*Nucula* (*Ennucula*) *quirica* Dall. Holotype, U. S. Nat. Mus. no. 208727; W. H. Dall, collector, ×6. Recent; Chugachik Bay, Cook's Inlet, Alaska, 60 fathoms. (p. 33)

This plate supplied by the United States National Museum, through the courtesy of H. A. Rehder

EXPLANATION OF PLATE 6

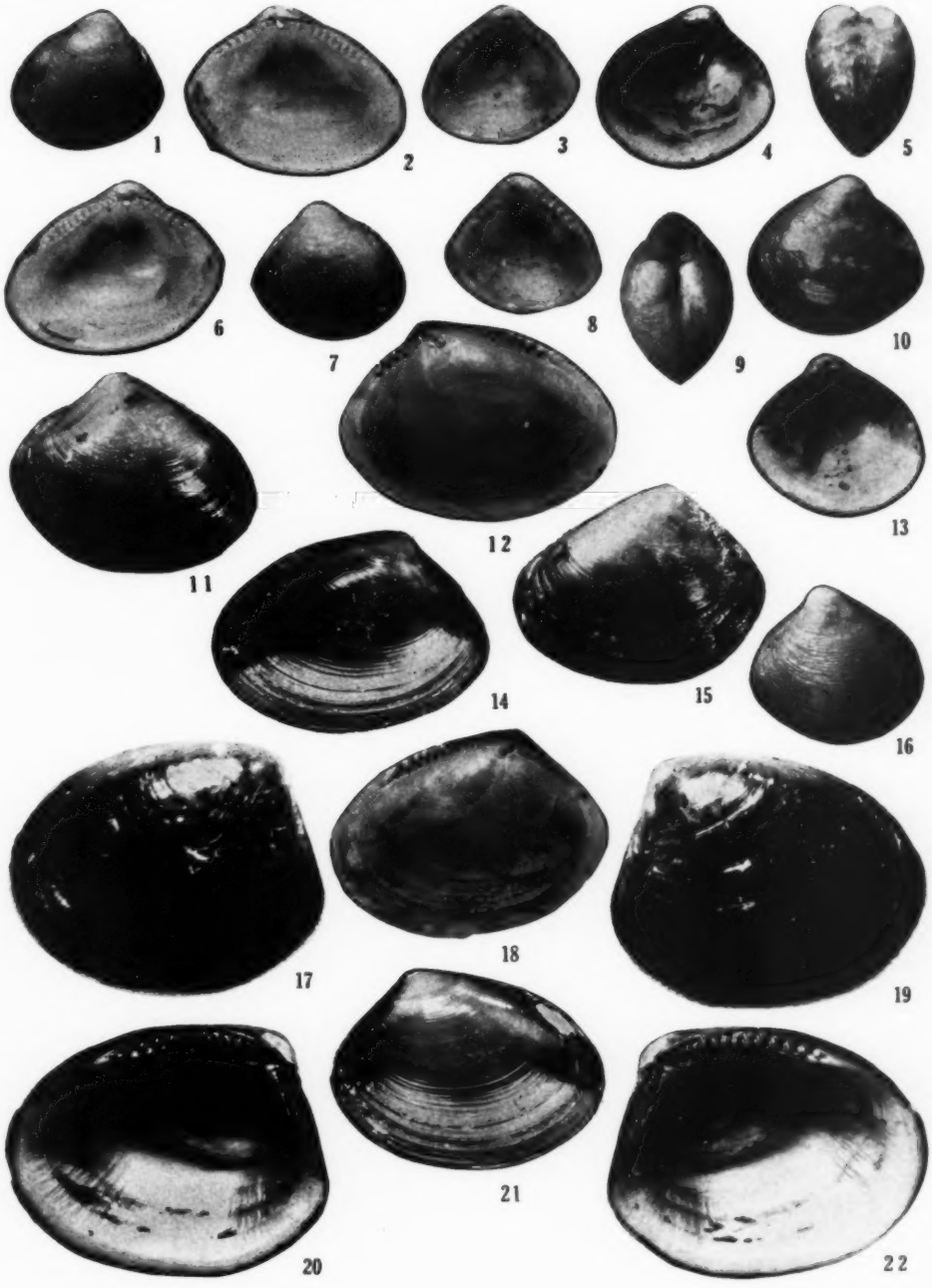
FIGS. *1–8, 11*—*Nucula* (*Nucula*) *exigua* Sowerby. Syntypes, British Museum (Natural History). Recent, "Bay of Caracas." *1–4, 6–7*, entire specimen; *5, 8*, odd valves, ×6; *11*, enlarged reproduction, ×2½, of protograph (Hanley, *Thes. Conch.*, vol. 3, pl. 229, fig. 136): enlargement in original figure, ×2; resultant enlargement in fig. 11, approximately ×5. Figs *1–8* supplied by British Museum (Natural History). (p. 36)

9, 10, 12, 13—*Nucula* (*Nucula*) *suprastriata* Arnold. Hypotype, Stanford Univ. Paleo. Type Coll. no. 6059, ×4½. Upper Pleistocene, Upper Potrero Canyon, about ¼ mile south of Pacific Palisades post office, Santa Monica, Los Angeles County, California. (p. 36)

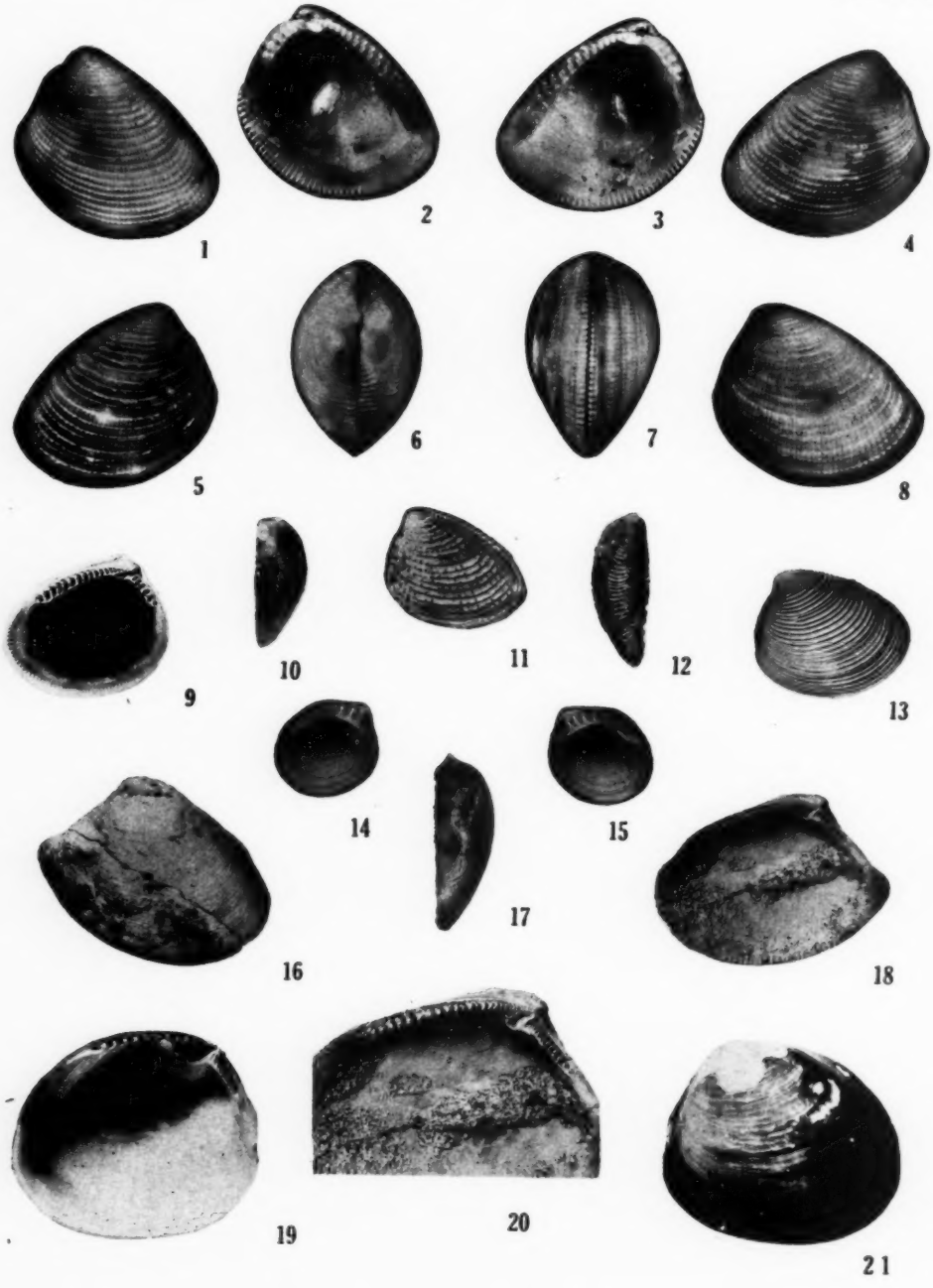
14, 15—*Nucula petriola* Dall (= *Cyrilla munita* Dall). Holotype, U. S. Nat. Mus. no. 271416, ×8. Recent, off Santa Rosa Island, California, 53 fathoms. (p. 39)

16–18, 20—*Nucula* (*Nucula*) *capayensis* Schenck, n. sp. Holotype, Univ. Calif. Mus. Paleo. no. 30196. Eocene, Capay Valley, Yolo County, California. *16, 18*, ×0.9; *17*, escutcheonal view, ×1.1; *20*, ×1.4, described by permission of B. L. Clark. (p. 34)

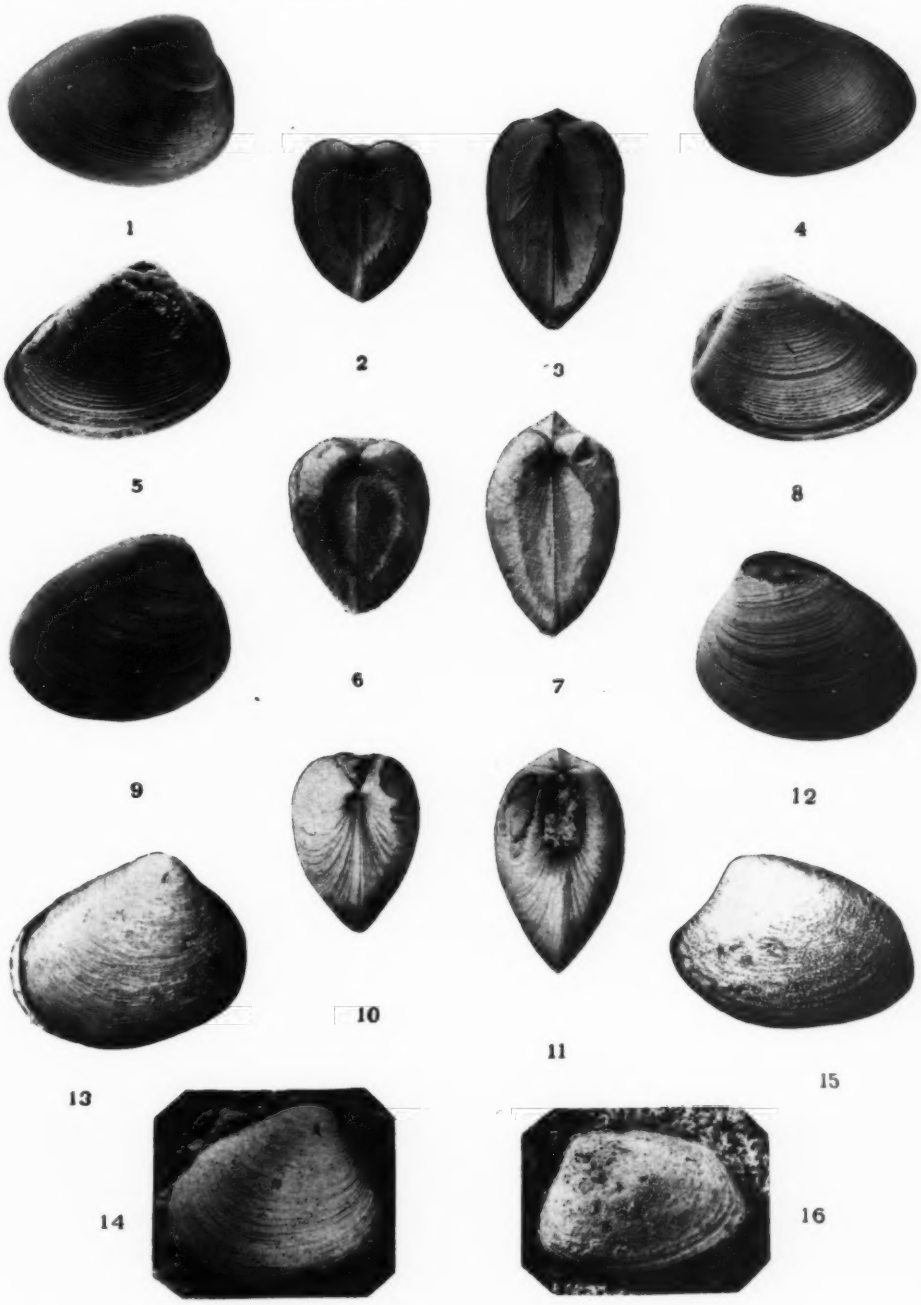
19, 21—*Nucula* (*Ennucula*) *bellotii* A. Adams. Holotype (?), British Museum (Natural History), ×2.2. Recent, "Arctic Seas." Photographs from British Museum (Natural History). (p. 30)



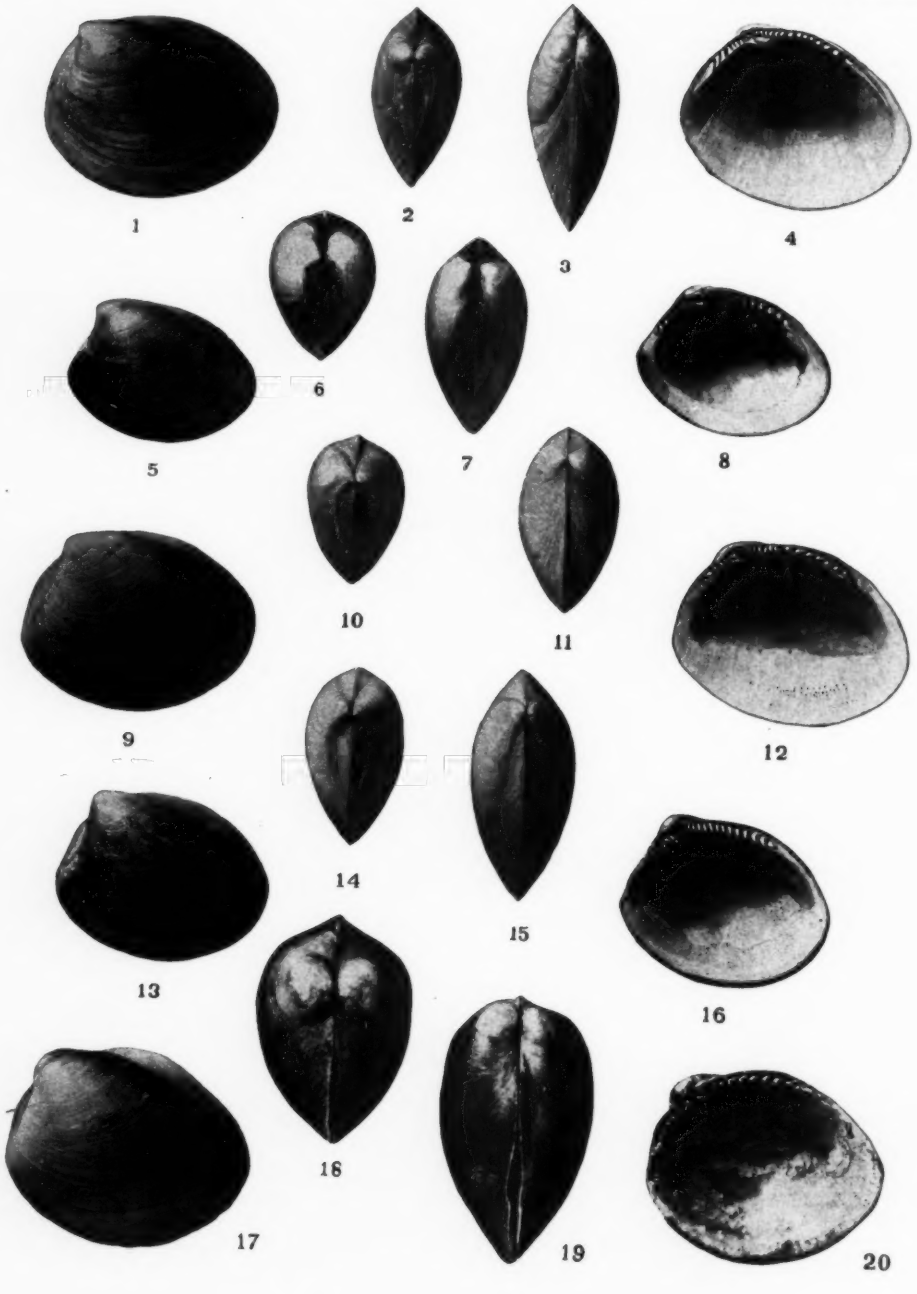
Schenck, Species of *Nucula*



Schenck, Species of *Nucula*



Schenck, Species of *Nucula*



Schenck, Species of *Nucula*

1922, Ohio Geol. Survey, ser. 4, Bull. 25, pp. 202–203. *Not* G. B. SOWERBY, JR., *1833*, Conch. Illustrations, Cat. Nuculae, pp. 3, 4, fig. 7. *Not* W. and H. ROGERS, *1837*, Am. Philos. Soc. Proc., n. ser., vol. 5, art. 14, p. 340.

"*Nucula*" *parva* McChesney. SCHENCK, *1934*, Mus. roy. Hist. Nat. Belgique Bull., t. 10, no. 40, p. 12.

?*Nucula beyrichi* GEINITZ, *1866*, (*not* V. Schauroth, 1854), Carbonformation und Dyas in Nebraska, p. 21, pl. 1, figs. 36–37.

Type material.—Neotype (of *Nucula parva* McChesney) no. 14518a, Walker Museum, University of Chicago.

Type locality.—Danville, Illinois, black shale overlying coal no. 7 of latest Allegheny or earliest Conemaugh age, according to J. Marvin Weller (letter of Jan. 4, 1936).

Material examined.—Three topotypes of *Nucula parva* McChesney from the Pennsylvanian of Danville, Illinois, in the Walker Museum, no. 14518. No specimen showing the interior was available.

Discussion.—"*Nucula*" *parva* McChesney, 1860, from the "Coal Measures" is not congeneric with the Eocene "*Nucula*" *parva* W. and H. Rogers, 1837, nor with the Recent Arctic bivalve "*Nucula*" *parva* G. B. Sowerby, Jr., 1841. As remarked elsewhere (17), the Paleozoic species is better considered a member of the genus *Nuculopsis* Girty than of the genus *Nucula* Lamarck. Topotypes of *parva* McChesney were placed at my disposal by Carey Croneis who informed me (letter dated May 16, 1935) that the holotype of the species was probably destroyed by fire; hence I hereby designate the specimen figured here (plate 7, figs. 1–4) as the neotype. McChesney's name is a primary homonym, and a new name must be proposed.

Description of neotype.—Shell medium size for genus; anterior dorsal margin gently convex, sloping to subacute anterior extremity; ventral margin strongly convex; posterior side straight, except for "pouting" of escutcheonal area; beaks closely appressed, orthogyrate; sculpture of low, concentric ribs, which are faint on the escutcheonal area but pronounced on the lunular area; interior not available.

Dimensions.—Length, 9.7 mm; height, 7.5 mm; thickness, 6.1 mm, umbonal angle, 101°.

Generic and subgeneric allocation.—This species, as well as all other Paleozoic nuculids that have come into my hands, have little in common with the genotype of *Nucula* (18). *N. croneisi* is more nearly re-

EXPLANATION OF PLATE 7

FIGS. *1–4*—*Nuculopsis* (*Palaeonucula*) *croneisi* Schenck, n. n. Neotype of "*Nucula parva*" McChesney, ×3. Pennsylvania; Danville, Illinois. (p. 24)

5–8—*Nuculopsis* (*Palaeonucula*) *welleri* Schenck, n. sp., ×4½. Mississippian; 1½ miles north of Marigold, Illinois. (p. 23)

9–12—*Nuculopsis* (*Palaeonucula?*) *okawensis* Schenck, n. sp., ×4. Mississippian; 1¼ miles northeast of Ruma, Illinois. (p. 23)

13, 14—"*Nucula*" *illinoiensis* Worthen, paratype. *13*, Drawing from photograph, ×3.5; *14*, photograph of specimen in matrix, ×3.0. Mississippian; Monroe County, Illinois. (p. 22)

15, 16—"*Nucula*" *illinoiensis* Worthen, holotype. *15*, Drawing from photograph, ×3.5; *16*, photograph of specimen in matrix, ×3.0. Mississippian; "Oolite bed of the St. Louis limestone, Monroe County, Illinois." (p. 22)

EXPLANATION OF PLATE 8

FIGS. *1–4*—*Nucula* (*Ennucula*) *tenuis* (Montagu). Virtual topotype, ×4. Recent, Loch Fyne, Scotland. Schenck Collection, no. 1587. (p. 33)

5–8—*Nucula* (*Ennucula*) *puelcha* D'Orbigny, 1842. Topotype of *Nucula uruguayensis* E. A. Smith, 1880, ×3. Recent, Stanford Univ. Paleont. Type Coll., no. 5689. (p. 30)

9, 12, 14, 15—*Nucula* (*Ennucula*) *tenuis* Montagu, ×4½. Recent; Nanoose Bay, British Columbia, 20 fathoms. Stanford Univ. Paleo. Type Coll; *9, 14, 15*, no. 5929; *12*, no. 5930. (p. 33)

10, 11, 13, 16—*Nucula* (*Ennucula*) *bellotii* A. Adams. Variation extreme commonly identified as *N. expansa* Reeve. Recent; Kostin sharr, Nova Zembla, 15–20 fathoms. *10, 11*, Stanford Univ. Paleo. Type Coll. no. 5932, ×2.5; *13, 16*, Stanford Univ. Paleo. Type Coll. no. 5931, ×3. (p. 30)

17–20—*Nucula* (*Ennucula*) *bellotii* A. Adams. Variation extreme commonly identified as *N. inflata* Hancock. Greenland, collected by Mörch. Schenck Coll. no 1586; *17, 20*, ×4; *18, 19* ×4¾. Recent. Photographs by A. Tchonravov retouched by E. H. Quayle. (p. 30)

lated to the genotype of *Nuculopsis* Girty, 1911, yet unlike *Nuculopsis girtyi* Schenck, the Illinois bivalve lacks strongly opisthogyrate beaks. In that character, it is like the genotype of *Palaeonucula* Quenstedt, 1930. The Paleozoic species resembles except for profile *Nuculopsis* (*Palaeonucula*) *hammeri* (Defrance) from the Jurassic, *Nuculopsis* (*Palaeonucula*) *strigilata* (Goldfuss) and *expansa* Wissmann from the Triassic of Europe. Hence, with the subgeneric placement of *croneisi* made here, *Palaeonucula* becomes both a Paleozoic and a Mesozoic subgenus.

Comparisons.—Girty (6) correctly held that "*Nucula*" *parva* McChesney is related to "*Nucula*" *wewokana* Girty, figured by him in U. S. Geological Survey Bulletin 544 (1915), pl. 13, figs. 6–8. Girty kindly placed topotypes of *wewokana* at my disposal. Although poorly preserved, these specimens suggest that *wewokana* is referable to *Palaeonucula* and prove that the species is distinct from *illinoiensis* and "*parva*" McChesney.

Girty implied, in 1915, that McChesney's species is related to "*Nucula*" *pulchella* Beede and Rogers (1), described from Cameron's Bluff, near Lawrence, Kansas, but a topotype of *pulchella* placed at my disposal by Norman D. Newell shows that the species are different.

Distribution.—The type locality of *Nuculopsis croneisi* at Danville, Illinois (11) has yielded well-preserved specimens of Pennsylvanian fossils. Meek and Worthen, Weller, Morningstar, and Schenck have cited occurrences from the Pennsylvanian or "Lower and Upper Coal Measures" of Arkansas, Illinois, Iowa, Missouri, Ohio, and Texas.

NUCULANA (SACCELLA) "PARVA" W. B. and H. D. Rogers), 1837

Nucula parva W. B. and H. D. ROGERS, *1837*, Am. Philos. Soc. Trans., n. s., vol. 5, p. 340. *Not* G. B. SOWERBY, JR., *1833*, Conch. Illust., Nuculae, p. 3–5, fig. 7.

Leda parva (Rogers). CLARK and MARTIN, *1901*, Maryland Geological Surv., Eocene, pp. 197–198, pl. 56, figs. 5–7a, with synonymy.—VAN WINKLE, *1921*, Bull. Am. Paleontology, vol. 8, no. 36, p. 7.

Type material.—Unknown.

Type locality.—Coggins Point, Virginia.

Discussion.—This species was described from strata now placed in the Nanjemoy formation. Clark and Martin (3) figured material from Woodstock, which they identified as *Leda parva* (Rogers). Their synonomy indicates that Conrad, in 1854, recognized that the species should not be allocated to *Nucula* but to "*Leda*." The Eocene species is thus a primary homonym not only of the Recent "*Nucula*" *parva* Sowerby but also of "*Leda*" *parva* Sowerby, one and the same species.

Henry A. Pilsbry informed me (letter dated May 23, 1935) that the type of "*Nucula*" *parva* Rogers is not known to exist in any museum.

No topotypes are available. Katherine van Winkle Palmer has been so kind as to place at my disposal several specimens of the species from the Wilcox (Sabine) Eocene of Woods Bluff, Alabama. Although these shells are well preserved, it is difficult to detect the chondrophore, since it is tucked up under the inner side of the umbones. As is well known, the species has strong concentric sculpture but lacks radial lines. It belongs to the genus *Nuculana* Link (typified by *N. rostrata* [= *Arca pernula* O. F. Müller]) and probably to the subgenus *Saccella* Woodring (type, *Arca fragilis* Chemnitz = *Leda commutata* Philippi); typical material of the subgenus is, unfortunately, not in hand for comparison. A new name is not proposed because of the probability that there is an available synonym.

NUCULANA PARVA (G. B. Sowerby), 1833

Nucula parva G. B. SOWERBY, JR., *1833*, Conch. Illus., Nuculae, pp. 3, 4, fig. 7.—REEVE, *1841*, Conch. Systematica, vol. 1, p. 110, pl. 85, fig. 7.—HANLEY, *1843*, Recent Bivalve Shells, p. 169.

Type material.—Unknown.

Type locality.—Melville Island, Arctic Ocean.

Discussion.—G. B. Sowerby, Jr., named as new the Recent pelecypod "*Nucula parva*" from Melville Island, where it was collected by Captain Parry (19, 7a). The protograph, though poor, leaves no doubt but that the species belongs to the family *Nuculanidae.*

NUCULA (NUCULA) DARELLA Dall, 1916 Plate 5, figures 1, 3, 7, 8

Nucula darella DALL, *1916*, U. S. Nat. Mus.

Proc., vol. 52, p. 394; *1921*, U. S. Nat. Mus. Bull. 112, p. 10.—KEEN, *1937*, *West North American Marine Mollusca*, p. 23.

Holotype.—U. S. Nat. Museum no. 111424.

Type locality.—Off San Diego, California, 822 fathoms, "Albatross" station 2923.

Discussion.—This species, here figured for the first time, is related to *Nucula* (*Nucula*) *atacellana* Schenck, the renamed *cancellata* Jeffreys, not Meek and Hayden. From *atacellana* it differs in having less conspicuous radial sculpture, in being more nearly trigonal in outline, and in having a somewhat heavier hinge in proportion to the size of the shell. From *exigua*, another related species, it differs in being more equilateral, in having anterior and posterior hinge teeth more nearly equal in number, and in the fainter radial sculpture. No specimens have been available for study.

NUCULA (NUCULA) ATACELLANA
Schenck, new name
Plate 5, figures 4, 5, 9, 10, 13, 16

Nucula reticulata JEFFREYS, *1876*, Annals and Mag. Nat. Hist., ser, 4, vol. 18, p. 429; *1879*, Zool. Soc. London Proc., p. 583. *Not* HINDS, 1843.

Nucula cancellata JEFFREYS, *1881*, Zool. Soc. London Proc., p. 951 (new name for *N. reticulata* Jeffreys not Hinds).—VERRILL, *1884*, Connecticut Acad. Arts & Sci. Trans., vol. 6, p. 280, 285.—VERRILL and BUSH, *1898*, U. S. Nat. Mus. Proc., vol. 20, p. 854, pl. 81, fig. 3, pl. 86, fig. 5.—JOHNSON, *1934*, Boston Soc. Nat. Hist. Proc., vol. 40, no. 1, p. 15. *Not* MEEK and HAYDEN, *1856*, Acad. Nat. Sci. Philadelphia Proc., vol. 8, p. 85.

Type material.—Lectotype, U. S. National Museum, Washington, D. C. Through the coöperation of Harald A. Rehder, a lectotype of "*Nucula reticulata*" is hereby chosen as that specimen figured on pl. 5, figs. 4, 5, 9, 10, 13, 16. It is from the "Porcupine" station described below.

Type locality (*here designated*).—"Porcupine" Expedition, 1869, off the northwestern coast of Ireland, 1476 and 1215 fathoms.

Discussion.—Specimens identified as this species are before me (Schenck Coll. 2096), from "Albatross" Station no. 2571, Georges Bank, Bering Sea. The soft parts of these specimens have been examined by Heath (8), who finds in this species the longest intestine encountered in any nuculid pelecypod which he has dissected. The shells have cancellate sculpture and crenulate ventral margins, thus allying the species with *Nucula rugulosa* G. B. Sowerby, *sculpturata* Sowerby, *rugosa* Odhner, *papillifera* Thiele, *sumatrana* Thiele, and others. *Nucula carlottensis* Dall (4) also has cancellate sculpture but differs from *atacellana* in outline, being more inequilateral; it appears to have more numerous hinge teeth, though this may not be a constant characteristic. The dimensions given for *carlottensis* are: height, 5.2, length 6.0, diameter 3.5 mm; for *atacellana* the corresponding dimensions are: "Long. 0.15; breadth, 0.175 poll.," which would indicate a length of approximately 4.0 mm.

NUCULA (PECTINUCULA) CANCELLATA Meek and Hayden, 1856

Nucula cancellata MEEK and HAYDEN, *1856*, Acad. Nat. Sci. Philadelphia Proc., vol. 8, pp. 85, 285.—STOLICZKA, *1871*, Palaeontologia Indica, Cret. Fauna of S. India, vol. 3, p. 327.—MEEK, *1876*, Invert. Cretaceous and Tertiary Fossils, U. S. Geol. and Geog. Survey, 9th Ann. Rept., Terr., p. 102, pl. 28, figs. 13 *a–e*.—BOYLE, *1893*, U. S. Geol. Survey Bull. 102, pp. 200, 201.—CORYELL and SALMON, *1934*, Am. Mus. Nat. Hist. Novitates, no. 746, pp. 6–7.

Nucula cancellata Meek and Hayden? RAVN, *1918*, Meddelelser om Grønland, Bd. 56, p. 344.

Type locality.—Moreau River, South Dakota; Upper Cretaceous.

Material examined.—Topotypes, U. S. National Museum no. 5879, Fox Hills formation of SE. ¼, Sec. 30, T. 13 N., R. 20 E. Specimens no. 5882 from same formation, NE. ¼, Sec. 17, T. 14 N., R. 20 E.

Type material.—The following report was submitted by John B. Reeside, Jr. (letter dated May 24, 1935):

> We have here (United States National Museum) the lots studied by Meek that should constitute the holotype and paratypes. There are no specimens, however, which now match the figure of the holotype, said by Meek to be a "perfect specimen" (valve?). One of the specimens in the type lot, and the only one to do so, matches the type figure exactly in size, but the shell at some time has been broken off the internal mold and only partly replaced. It is my suspicion that this may be the holotype, the original of pl. 28, figs. 13*a*, *c*, of the Upper Missouri report (vol. 9), though I am afraid it can never be proved. The original of figs. 13 *d*, *e* is identified with certainty.
>
> U. S. National Museum catalogue no. 434 covers a lot of seven specimens from Moreau River

and Long Lake, South Dakota. The original label in Meek's handwriting confirms the association of material from the two localities. The lot was marked, probably in the eighties, as containing the originals of figs. 13*d*, *e*, and doubtfully of figs. 13*a*, *c* (the holotype). The original of fig. 13*b* was not noted even then. U. S. National Museum catalogue no. 1931 covers a lot of nine specimens, one of which was erroneously marked at some time as the original of figs. 13*d*, *e*. This lot appears certainly to contain paratypes, but I find no specimens that can be identified as originals of figures. The material in both lots is mainly internal molds and as far as it goes fits Meek's description quite well.

In brief, Meek's holotype was not definitely identifiable in the eighties, though his type lots were then and still are extant. Possibly the damaged specimen referred to above is a remnant of the holotype.

Description of topotypes.—Shell medium size for subgenus; anterior dorsal margin gently convex; anterior extremity bluntly rounded; ventral margin convex; posterior side straight, sloping, giving only slight rostrate appearance to smaller specimen; beaks opisthogyrate; radial ribs strong, separated by narrow interspaces, and when crossed by concentric ribs and growth undulations produce reticulate sculpture; ribs do not cross escutcheonal area; interior not completely exposed; inner ventral margin crenulate. The approximate measurements are as follows:

DIMENSIONS OF N. CANCELLATA

Specimen U. S. Nat. Mus.	Length in mm	Height in mm	Thickness in mm	Ratio of height to length in per cent
5879	10.7	7.7		72
5882	20.2	15.6	13.1	77

Comparisons.—In the original description (12) the authors compared the species with "*N. pectenata* of Sowerby." *Nucula* (*Pectinucula*) *pectinata* Sowerby, figured elsewhere (Mus. roy. Hist. Nat. Belgique Bull., tome 10, no. 20, pl. 3, figs. 1, 1*a–c*, 1934), is a common species in the Gault (Cretaceous) of Europe. It is recorded also from the upper Albian of the north Caucasus (13). The American and European species differ in outline, and *cancellata* has a less sunken escutcheonal area. *Nucula radiatocostata* Nagao (Jour. Fac. Sci. Hokkaido Imp. Univ., ser. 4, vol. 2, no. 1, pp. 27–28, pl. 5, fig. 12, Nov. 1932) is based on poor material, but it seems to be a *Pectinucula*, as does *Nucula luciae* G. Seguenza (R. accad. Lincei, Cl. sci. fis. Atti, ser. 3, vol. 12, p. 156, pl. 12, fig. 7, 1882) from the middle Cretaceous of Italy. *Nucula bidorsata* Stoliczka (Cret. Fauna S. India, III, pp. 329–330, pl. 17, figs. 22, 24–27, 1871) and *N. crassicula* Stoliczka (*ibid.*, p. 329, pl. 17, fig. 23) are probably related to the American species. The subgenus *Pectinucula* may not occur in strata older than Cretaceous. Its distribution during the late Cretaceous was world-wide.

NUCULA (NUCULA) LATTORFIANA
Schenck, new name

Nucula ovata Deshayes. NYST, *1836*, Rech. coq. foss. de Kleyn-Spauwen et Housselt, p. 13, no. 31. *Not* DESHAYES, *1824*, *nor* MANTELL, *1822*, *nor* VERRILL and BUSH, *1898*.

Nucula similis Solander. VINCENT, *1886*, Soc. royale malac. Belgique Ann., 4 ser., t. 1 (tome 21), p. 13. *Not Nucula similis* SOWERBY, *1818*.

Nucula rugulosa von KOENEN, *1893*, Geol. Landesanstalt Abh., Bd. 10, Heft 5, pp. 1115–1116, pl. 73, figs. 19–21, 22a, 22b, 23. *Not* G. B. SOWERBY, *1833*, Conch. Illus., Nuculae, p. 5, fig. 19.

Holotype.—Possibly in University of Göttingen, Germany.

Type locality.—Lattorf, Germany. Lattorfian (lower Oligocene).

Material examined.—Two topotypes (Schenck coll. no. 938); several specimens from the lower Tongrian, Province of Limbourg, Belgium, in the Musée Royal d'Histoire Naturelle de Belgique.

Discussion.—This species is described fully by von Koenen (10). The excellent figures leave no doubt as to the general characteristics of the species. In length, some specimens are as much as 22.0 mm, although the species is readily identified when specimens 15.0 mm or less are in hand. The heavy *Inoceramus*-like undulations are pronounced on all of the specimens; these are waves similar to those on the Miocene species, *Nucula haesendoncki* Nyst. The Lattorfian species resembles *Nucula regnorum* Wrigley but differs from it in outline and, according to Wrigley (letter dated June 2, 1935), in having a feebler radial sculpture. *Nucula comta* Goldfuss, a Chattian species, differs in profile and in having lower and regular growth undulations. *Nucula peregrina* Deshayes, another Oligo-

cene species, belongs to a different subgenus than *Nucula lattorfiana*. Nor need specimens be confused with *Nucula duchastelii* Nyst,[1] often taken as an index fossil of the Rupelian of western Europe.

Wood figured (21) as *Nucula similis* Sowerby a specimen supposedly from Barton. I have not had an opportunity to compare his specimen with Sowerby's material, but L. R. Cox states (written communication dated December 1, 1933) that in his opinion the specimens figured by Wood as *N. similis* (and in any case the larger one) belong to that species restricted to Sowerby's figure 10. No matter what may be done about delimiting Sowerby's species, the fact remains that the specimens of *similis* are similar to, but not conspecific with, the lower Tongrian of Belgium and the Lattorfian of Germany, since the sculpture and the less impressed escutcheonal area of *lattorfiana* will distinguish it from *similis*.

NUCULA (NUCULA) RUGULOSA
G. B. Sowerby, 1833

Nucula rugulosa G. B. SOWERBY, Jr., *1833*, Conch. Illustrations, Nuculae, p. 5, fig. 19.—HANLEY, *1843*, Cat. Recent Bivalve Shells, p. 171, pl. 20, fig. 10.—CATLOW and REEVE, *1845*, The Conch. Nomenclator, p. 54.—HANLEY in SOWERBY, *1860*, Thesaurus, vol. 3, pt. 20, p. 149.—H. & A. ADAMS, *1858*, Genera Recent Mollusca, p. 545.—MELVILL and STANDEN, *1907*, Zool. Soc. London Proc. for 1906, p. 792.—MELVILL, *1906*, Zool. Soc. London Proc., pt. 2, p. 702.—PRASHAD, *1933*, Archiv f. Naturgeschichte, n. f., Bd. 2, Heft 1, pp. 131, 132, pl. 1, fig. 11.

Type material.—Probably British Museum (Natural History).

Type locality.—Exact locality unknown.

Discussion.—No type locality is given either by Sowerby or by Hanley (*7b*). The identifications by Melvill and Standen and Prashad (*supra cit.*) are probably correct, and, if so, then the species is Indo-Pacific. Hence the species is not, as Hanley (1860) affirmed, a Mediterranean "variety" of *Nucula nucleus* (Linné).

A. Wrigley states (letter dated June 2, 1935) that in the British Museum (Natural History) there is only one tablet labelled "*Nucula rugulosa* G. B. Sowerby, I." It bears two specimens, one of *N. nucleus*, the other a shell which corresponds with the Sowerby description. Wrigley adds that an essential character, not mentioned or figured by Sowerby, is the marked anastomosing of the concentric ridges, which are slightly nodular where crossed by the rays. There are 4 rays per millimeter at the ventral margin. The British Museum specimen is not marked as a holotype, nor does the tablet bear any indication of origin or locality.

This species may prove to be related to *N. sculpturata* Sowerby (and its possible synonym *N. rugosa* Odhner) and to *N. papillifera* Thiele (in Thiele and Jaeckel, "Valdivia" Exp. Bd. 21, Heft 1, pp. 200–201, T. II, fig. 49, 1931).

NUCULA (NUCULA) MARSHALLI
Schenck, new name

Nucula uruguayensis MARSHALL, *1928*, U. S. Nat. Mus. Proc., vol. 74, no. 2762, art. 17, pp. 6, 7, pl. 4, figs. 13–15. *Not* E. A. SMITH, *1880*, Annals and Mag. Nat. Hist., ser. 5, vol. 6, no. 34, p. 320.

Holotype.—No. 368228, U. S. National Museum, Washington, D. C.

Type locality.—Coast of Maldonado, Uruguay, in the estuary of the Rio de la Plata.

Material examined.—Paratype, U. S. Nat. Mus. no. 368229, one left valve.

Discussion.—This species is based on specimens with weak radial sculpture, distinct concentric ornamentation, and a crenulate inner ventral margin. The profile of the holotype offers a ready means of separating the species from *Nucula nucleus* (Linné). The concentric ornamentation distinguishes *marshalli* from *Nucula nitidosa* Winckworth, *N. truncula* Dall, and *N. proxima* Say. From *Nucula crenulata* Adams, the Uruguayan species differs in profile and ornamentation. *Nucula sculpturata* G. B. Sowerby, 1904, a species from South Africa, also has strong concentric ribs, but it lacks the truncate posterior side of *marshalli*. The species from Uruguay seems to be close to *Nucula exigua* Sowerby, 1832, from the "Bay of Caraccas" (probably in

[1] This species is frequently described and figured as *Nucula chastelii* Nyst. Especially complete information is given by C. L. Fridolin Sandberger in *Die Conchylien des Mainzer Tertiärbeckens*, pp. 342–343, pl. 28, figs. 7, 7a, 7b, Wiesbaden, 1863.

the Caribbean province), but authentic topotypes are not in hand for direct comparison.

NUCULA (ENNUCULA) PUELCHA D'Orbigny, 1842
Plate 8, figures 5–8

Nucula puelcha D'ORBIGNY, *1842*, Paleont. de l'Amérique méridionale, p. 162, no. 175. (*fide* D'Orbigny, 1846)—D'ORBIGNY, *1846*, Voyage dans l'Amérique méridionale, vol. 5, part 3, Mollusques, p. 624, pl. 84, figs. 24–26.—HANLEY, *1860*, Mon. family Nuculidae, in SOWERBY, Thes. Conch., vol. 3, p. 156, pl. 230 (Nuculidae 5), fig. 149.

Nucula puelchana DESHAYES, *1839–57*, Traité élém. Conch., t. 2, p. 307.

Nucula uruguayensis E. A. SMITH, *1880*, Annals and Mag. Nat. Hist., ser. 5, vol. 6, p. 320.—PILSBRY, *1897*, Nautilus, vol. 11, no. 1, p. 9.

Nucula felipponei MARSHALL, *1928*, U. S. Nat. Mus. Proc., vol. 74, p. 6, pl. 4, figs. 10–12.

Type material.—Perhaps in Muséum National, Paris.

Type locality.—San Blas Bay, South America.

Material examined.—Topotype of *Nucula uruguayensis* Smith.

Discussion.—This species, based upon a shell 7 mm long and said by d'Orbigny to be related to *Nucula obliqua*, was well figured (exterior only). The type locality is "le fond de la baie de San-Blas, au nord de la Patagonie, sur les bancs de sable vaseux qui se découvrent à marée basse. Elle y rare." Hanley (1860) says that [D'Orbigny's] "types of this species, which remind us of *nitida* and *convexa*, are in sorry condition, without epidermis, and worn smooth." The types probably "reminded" Hanley of the species named because all belong to the family Nuculidae.

Smith's species was named for material from 36° 47′ south latitude and 55° 17′ west longitude, in 28 fathoms, off the estuary of the Rio de la Plata, Uruguay, and was compared with *Nucula obliqua* Lamarck, which Iredale took as the type of his *Ennucula* (16*b*). A topotype of *uruguayensis* Smith was figured and described by Marshall as *Nucula felipponei*. A topotype of Smith's species, no. 5869, paleontological collection at Stanford University, measures 9.2 mm in length, 7.0 mm in height, and 5.2 mm in thickness. It is the shell figured on plate 8, figures 5–8. The inner ventral margin is smooth and the chondrophore is oblique.

NUCULOPSIS (PALAEONUCULA) EXPANSA (Wissmann) in Münster, 1841

Nucula expansa WISSMANN, *1841*, in Graf zu Münster, Beiträge zur Petrefacten-Kunde, Bd. 4, p. 84.—BITTNER, *1895*, K. k. geol. Reichsanstalt Abh., Bd. 18, Heft 1, pp. 140, 141, pl. 17, figs. 25–33.

Nucula subcordata D'ORBIGNY, *1849*, Prodrome, vol. 1, p. 199 (*fide* DIENER, *1923*, Fossilium Catalogus, I: Animalia, Pars 19, p. 156.

Type material.—Unknown.

Type locality.—St. Cassian, Switzerland.

Material examined.—Topotype (Schenck coll. 943) and several topotypes in various European museums.

Discussion.—This Triassic species was named in the following manner (14):

> 4. *Nucula cordata* Goldf. Taf. VIII, fig. 11a,b. sehr vergrössert.
>
> Diese Art, welche Herr Dr. Wissmann für eine eigne Species hielt und *N. expansa* nannte, kommt so sehr mit der von Goldfuss Taf. 125, fig. 6a,b,c. abgebildeten und pag. 155 als *N. cordata* beschriebenen Art überein, dass ich bei genaarer Vergleichung der Original-Exemplare durchaus keinen wesentlichen Unterschied finden, ja sie kaum als Varietäten trennen kann. . . .

A specimen is well figured by Bittner (2). The species is trigonal, with fine concentric ribs, and orthogyrate beaks. The relationships of the species are uncertain because the Triassic species need revision by a modern taxonomist.

NUCULA (ENNUCULA) BELLOTII A. Adams, 1856
Plate 6, figures 19, 21; Plate 8, figures 10, 11, 13, 16–20

Nucula bellotii A. ADAMS, *1856*, Zool. Soc. London Proc., pt. 24, p. 51.—HANLEY, *1860*, in SOWERBY, Thes. Conch., vol. 3, pp. 162, 163, pl. 229 (IV) fig. 128.

Nucula inflata HANCOCK, *1846*, Ann. and Mag. Nat. Hist. vol. 18, p. 333, pl. 5, figs. 13, 14.—HANLEY, *1860*, in SOWERBY, Thes. Conch., vol. 3, Pt. 20, p. 162, pl. 229, figs. 115, 116.—E. A. SMITH, *1877*, Ann. and Mag. Nat. Hist., 4 ser., vol. 20, p. 141. *Not* J. de C. SOWERBY, *1827*, Min. Conch., vol. 5, p. 103, pl. 554, fig. 2 (= *Cuspidaria inflata*). *Not* WISSMANN, 1841.

Nucula tenuis Montagu, var. *inflata*, JEFFERYS, *1863*, British Conch., vol. 2, pp. 151, 152.—SOOT-RYEN, *1932*, *Maud* Exped., vol. 5, no. 12, p. 5, pl. 1, fig. 5.

Nucula tenuis inflata Hancock. JOHNSON, *1934*, Boston Soc. Nat. Hist. Proc., vol. 40, no. 1, p. 15.

Nucula expansa REEVE, *1855*, in BELCHER, The Last of the Arctic Voyages, p. 397, pl. 33, fig. 2.—JEFFREYS, *1863*, Brit. Conch., p. 152.—

M. SARS, *1865*, Om de i Norge forekommende Fossile, p. 36, pl. 2, figs. 52–55 (as var. *expansa*).—CROSSE, *1877*, Jour. Conchyl., vol. 25, p. 118.—DALL, *1895*, Wagner Free Inst. Sci. Trans., vol. 3, pt. 3, p. 577.—I. S. OLDROYD, *1924*, Stanford Univ. Publ. Geol. Sci., vol. 1, no. 1, p. 14, pl. 13, figs. 6, 7. *Not* WISSMANN, *1841*, in MÜNSTER, Beiträge zur Petrefactenkunde, Bd. 4, p. 84.

Nucula tenuis Mont. var. *expansa* Reeve. G. O. SARS, *1878*, Bidrag til Kunds. om Norges Artiske Fauna, I, pp. 33, 34.—LECHE, *1883*, *Vega*-Expeditionens Veten. Iakttagelser, Bd. 3, p. 449.—KRAUSE, *1885*, Archiv f. Naturgeschichte, vol. 51, Bd. 1, p. 21.—COLLIN, *1886*, Dijmphna-Togtets zool.-bot. Udbytte, Kjøbenhavn, p. 12.—A. JENSEN, *1905*, Meddelelser om Grönland, vol. 29, p. 299, 308, 316.—DALL, *1916*, Check-list of the Recent bivalve mollusks (publ. by Southwest Mus.), p. 9.—T. SOOT-RYEN, *1932*, Sci. results, Norwegian North Polar Exped. with the *Maud*, vol. 5, no. 12, pp. 4, 5, pl. 1, figs. 3, 4, 6.

?Nucula tenuis expansa Reeve. DALL, *1921*, U. S. Nat. Mus. Bull. 112, p. 9.—I. S. OLDROYD, *1924*, Puget Sound Biol. Sta. Pub., vol. 4, p. 5.—HATAI, *1936*, Biogeographical Soc. Japan Bull., vol. 6, no. 12, p. 131.

?Nucula expansa Reeve. DALL, *1897*, Nat. Hist. Soc. British Columbia Bull. 2, art. 1, p. 6.

Nucula quirica DALL, *1916*, U. S. Nat. Mus. Proc., vol. 52, p. 394; *1921*, U. S. Nat. Mus. Bull. 112, p. 10.

Type locality.—Of *bellotii*, "Arctic seas"; of *inflata* Hancock, a small bay in a deep inlet on the west coast of Davis Strait (lat. 66° 30′ north, long. 68° west); of *expansa* Reeve, probably Northumberland Sound, Arctic Ocean, approximately at 77° north latitude, 96° west longitude, according to the Scott Polar Research Institute, this locality being in the northerly part of the Grinnell Peninsula between Pioneer Island and Cape Sir John Franklin; of *quirica* Dall, Chugachik Bay, Cooks Inlet, Alaska, in 60 fathoms, gravelly bottom.

Type material.—Of *bellotii*, British Museum (Natural History); of *inflata* Hancock and *expansa* Reeve, proterotypes unknown; of *quirica*, U. S. National Museum, cat. no. 208727.

Discussion.—The original material of *Nucula bellotii* was collected by Sir E. Belcher. G. C. Robson, of the British Museum, informs me (letter dated July 13, 1936) that the types appear to be two specimens from the "*Mus. Cumingianum.*" He writes further as follows:

> They are not marked as such [types] but correspond fairly well with the description [by Hanley], and the larger specimens, though light olive and not the deep color shown in Thes. Conch., seem to come pretty near the form which the various writers had in view. The dimensions of the largest specimen agree fairly well, but there are certain slight differences in shape, and a prominent white posterior spot of erosion is not shown. I cannot help feeling that these shells are the types, though one could wish for more exact indication. I perhaps ought to add that Hanley's figure looks as though it might be generalized from the two specimens.

The presumed type of *bellotii* is figured here (Plate 6, figures 19, 21). The shell has the following dimensions: length, 15.3 mm; height, 12.7 mm; thickness, 4.7 mm.

Hanley (1860), Crosse (1877), and such other writers as Dall and Oldroyd, who followed their lead, have considered that *Nucula bellotii* A. Adams, 1856, is conspecific with *N. expansa* Reeve, 1855; so far as I can determine from a study of Arctic material, this view is probably correct. As I shall show, Reeve's species is a synonym of the earlier *N. inflata* Hancock; both of these names are primary homonyms, the one of *N. expansa* Wissmann, the other of *N. inflata* Wissmann. If they should prove distinct from *bellotii*, a new name would be needed, for there appears to be no other available synonym; Dall's citation of "*Nucula lucida* Gould" was not supported by evidence, and *lucida* seems, moreover, to be a *nomen nudum*. R. Winckworth states (letter dated May 6, 1936) that Mörch, in Grönlands Blöddyr (p. 20) gives *N. tenuis* "Gray" and *N. obliquata* Beck as synonyms of *N. inflata* Hancock, but that possibly "*N. obliquata* Beck" was not published. *Nucula quirica* appears to be a synonym of *N. bellotii* in the strict sense and hence would not qualify as an available synonym if the *expansa-inflata* complex were separated from *bellotii* as here conceived.

There has been not a little difference of opinion as to the identity of "*inflata*" and "*expansa*." Soot-Ryen (1932, p. 4), for example, identifies as "*inflata*" specimens with a dark-brown periostracum, whereas he called shells with a light-yellowish periostracum "*expansa*"; the original description of the latter, however, gave the color as shining gray-green, while the original description of "*inflata*" mentions a greenish-yellow epidermis. Torrell, Jeffreys, M. Sars, G. O. Sars, Dautzenberg and Fischer, and

many other authorities, on the other hand, have considered the two species to be identical. In this I concur, after making a biometrical study of abundant material from the Arctic: the color of the periostracum is variable; degree of inflatedness is not a specific criterion; and neither the ratio of height to length (and consequently profile) nor of thickness to length is to be relied upon in separating "*expansa*" from "*inflata*."

The specimens figured on plate 8 represent two extremes of profile. The virtual topotype of "*inflata*" shown in figures 17–20 is a small shell donated by R. Winckworth. It has the following dimensions: Length, 8.0 mm; height, 6.5 mm; thickness (both valves), 4.6 mm. The distinctive antero-dorsal profile—giving a somewhat "winged" appearance to the shell—is clearly shown in figure 17. The periostracum is greenish brown. The shell is imperfectly preserved on the interior, making impossible the determination of the muscle scar pattern; the numerous small punctations shown by the artist probably represent shell imperfections rather than scars.

The specimens shown in figures 10, 11, 13, and 16, all from Nova Zembla, may be described as follows: dorsal margin gently arched, no. 5932 being more convex upwards than 5931 and both more so than *tenuis;* anterior extremity bluntly rounded; ventral margin smooth, convex; posterior side straight to gently arched outward; exterior with numerous growth undulations but lacking concentric ribs; beaks opisthogyrate, appressed; escutcheonal area faintly defined; muscle scars clearly visible (fig. 16). Dimensions are given in the following table:

DIMENSIONS OF NUCULA (ENNUCULA) BELLOTII

Specimen (Stanford) Univ.)	Length in mm	Height in mm	Semi-thickness in mm	No. of teeth*		Umbonal angle, in degrees	Ratio of height to length
				Ant.	Post.		
5931	10.4	8.2	3.0	20	8	110	79%
5932	9.4	7.8	2.6	18	6	115	83%
9901	10.4	8.2	3.0			110	79%

* Left valve only.

In addition, material from the following localities has been studied: from Kings Bay, in 25 fathoms; Smeerenburg Bay and Storfjord (Whalerspynt) in 20–40 fathoms; Spitsbergen; Kodiak Island, Alaska (questionable identification); Ramfjord, Norway; Aukpadlartok, north Greenland, in 250 fathoms, fine clay; from 71° 39′ N., 157° 15′ E., 10 fathoms, in brown clay; from 70° 14′ N., 170° 17′ E., 12 fathoms; Illartlek, Öberg, Greenland, in 15–20 fathoms; Godhavn, Greenland, 15–35 fathoms. These numerous specimens demonstrate the variability of the shell profile and color of epidermis, from the extreme shown by figures 13 and 16 (plate 8) to that of figures 17 and 20. The degree of robustness of the hinge, the character of the chondrophore, the number of teeth, and other characters were studied in the attempt to ascertain if there are two biological units represented in the collections. No constant set of morphologic features could be discovered, either to differentiate "*inflata*" from "*expansa*" or to separate the two from *bellotii*.

Comparisons.—Nucula bellotii attains a length of 16 millimeters, in contrast to the smaller *tenuis*. In profile also the two species differ, *tenuis* being longer in proportion to height, with lower beaks. Most specimens of *bellotii* have a "winged" appearance along the antero-dorsal margin, best illustrated in plate 8, figure 17. Dautzenberg and Fischer (5) summarize the differences thus:

> Le *N. inflata* = *N. expansa* Reeve est une forme boréale généralement admise comme variété du *N. tenuis*, plus grande, plus haute, plus triangulaire, moins oblique, plus renflée, et à sommets plus proéminents.

Distribution.—Nucula bellotii is widely distributed in the Arctic Ocean and as fossil (probably Pleistocene) in Greenland. In addition to the occurrences given above, Jensen (1905) records the species from Cape Dalton, Turner Sound, Hurry Inlet, southeast of Sabine Island (110 fathoms), and MacKenzie Bay. The species may occur

rarely in the Boreal marine molluscan province, and even more sporadically in the Trans-Atlantic and Celtic provinces, but it is questionable whether or not it occurs in the Lusitanian, Japonic, and Californian provinces.

NUCULA (ENNUCULA) QUIRICA Dall, 1916
Plate 5, figures 17, 19, 20, 22

Nucula quirica DALL, *1916*, U. S. Nat. Mus. Proc., vol. 52, p. 394; *1921*, U. S. Nat. Mus. Bull. 112, p. 10.—KEEN, *1937*, West North American Marine Mollusca, p. 23.

Holotype.—U. S. Nat. Museum no. 208727.

Type locality.—Chugachik Bay, Cooks Inlet, Alaska, in 60 fathoms, gravelly bottom.

Discussion.—This species, which is here figured for the first time, appears to be a synonym of *N. bellotii* (see above). Judging from the photograph of the holotype, the only character which might be used in separating it from other West Coast species is the series of faint radial markings visible on the interior of the shell; this character is not mentioned by Dall in his original description. All of the diagnostic characters cited by Dall fall within the range of variation of *N. bellotii*. The dimensions of *quirica* are: Length, 8; height, 6; diameter, 3.5 mm.

NUCULA (ENNUCULA?) LINKI Dall, 1916
Plate 5, figures 2, 6, 11, 15

Nucula linki DALL, *1916*, U. S. Nat. Mus. Proc., vol. 52, p. 394; *1921*, U. S. Nat. Mus. Bull. 112, p. 10.—KEEN, *1937*, West North American Marine Mollusca, p. 23.

Holotype.—U. S. Nat. Mus. no. 107649.

Type locality.—Off Point Fermin, California (not "Lower California" as given in the original), 24 fathoms, mud, U. S. Bureau Fisheries "Albatross" station 3034.

Discussion.—Through the courtesy of the United States National Museum, this species is here figured for the first time. The species would appear to be distinguished from other West American representatives of the subgenus by the large, circumscribed lunule, the subtriangular outline, and the compressed chondrophore, which is less obliquely placed than those of other Ennucula.

NUCULA (ENNUCULA) TENUIS (Montagu), 1808
Plate 8, figures 1–4, 9, 12, 14, 15

Arca tenuis MONTAGU, *1808*, Test. Brit. Supplement, p. 56, pl. 29, fig. 1.

Nucula tenuis Montagu. HANLEY, *1860*, *in* SOWERBY, Thes. Conch. vol. 3, p. 161, pl. 229, figs. 140, 141.—JEFFREYS, *1879*, Zool. Soc. London Proc., p. 581.—DALL, *1885*, U. S. Geol. Surv. Bull. 24, p. 198.—DAUTZENBERG and FISCHER, *1912*, Res. Com. Sci. Monaco, fasc. 37, p. 392–395.—ANTEVS, *1928*, För. Geol. Fören. i Stockholm, Bd. 50, H. 4, p. 493.—HATAI, *1936*, Biogeographical Soc. Japan Bull., vol. 6, no. 12, p. 131.

Nucula tenuis. GOULD, *1841*, Report on the Invert. of Mass., p. 105.—HANLEY, *1843*, Ill. and des. cat. rec. bivalve shells, p. 171–172.

Nucula tenuis Möller. MÖRCH, *1853*, Cat. conchy., fasc. 2, p. 43.

Nucula tenuis tenuis Montagu. JOHNSON, *1934*, Boston Soc. Nat. Hist. Proc., vol. 40, no. 1, p. 15.

Type material.—Unknown.

Type locality.—Shore near Dunbar, south side of the mouth of Firth of Forth, about 30 miles east of Edinburgh, Scotland, 56° north, 2° 30′ west.

Material examined.—Specimens (virtual topotypes) from Loch Fyne, Scotland; Eastport, Maine, and others.

Figured specimens.—R. Winckworth kindly supplied the specimens figured on plate 8, figs. 1–4. The dimensions in millimeters of the specimen illustrated in figs. 1–3 are: length, 7.7; height, 6.0; thickness, 3.2. The left valve (fig. 4) is 7.6 mm long; 5.8 mm in height; semithickness, 1.8 mm. These shells correspond fairly well to the original description, except that there are about 16 anterior and 6 posterior teeth.

Comparisons.—The specimens available for inspection have smooth inner ventral margins and lack distinct concentric lines; they have oblique chondrophores and show no traces of radial ribbing. Hence, they cannot be placed in *Nucula, sensu stricto*, along with such species as *Nucula nucleus* (Linné), *groenlandica* Posselt, *proxima* Say, *decussata* Sowerby, *nitidosa* Winckworth, and many others. On the contrary, *tenuis* is more closely related to *Nucula obliqua* Lamarck, the genotype of *Ennucula* Iredale, 1931. *Nucula bellotii* Adams is allied to *tenuis*, and they may intergrade at the peripheries of their respective geographic ranges.

Discussion.—R. Winckworth states (letter dated May 6, 1935) that the holotype of *tenuis* is not in the British Museum (Natural History), but that the original description and figure fit the British species, notwithstanding the fact that many of Laskey's alleged finds at Dunbar are certainly not British and are probably attributable to ballast. The literature carries many citations to this species, but some of them are to misidentified specimens, such as a left valve figured by I. S. Oldroyd from the eastern North Pacific Ocean (15). Because of such errors, one may be skeptical of some of the numerous records of the species. It would be interesting to learn if Antevs (1928) was correct in giving its bathymetric range as from 2 to 1200 meters. Finally, we need to know how much of the dispersal is due to natural causes and how much to man.

Specimens from the eastern North Pacific Ocean.—The Recent shells no. 5929 and 5930 figured on pl. 8, figs. 9, 12, 14, 15, are from 20 fathoms in Nanoose Bay, British Columbia, and are like the many other representatives of the species in the Aleutian and Californian provinces. The dimensions of these hypotypes are as follows:

DIMENSIONS OF NUCULA (ENNUCULA) TENUIS

Specimen (Stanford Univ.)	Length in mm	Height in mm	Thickness in mm	No. of teeth* Ant.- Post.	Ratio of height to length in per cent
5929	7.4	5.9	3.3		80
5930	7.8	5.8		16 8	75

* Left valve only.

I. S. Oldroyd recently collected several hundred specimens from British Columbia. These exhibit a considerable range of variation. Thus, a large number of the shells from Nanoose Bay agree exactly with specimens from the North Sea, whereas others differ somewhat in profile and character of the hinge. The largest specimen measured from the Puget Sound region is 10.5 mm in length. The species is reported to range southward to Coronado Islands.

NUCULA (ENNUCULA) CARDARA
Dall, 1916
Plate 5, figures 12, 14, 18, 21

Nucula cardara DALL, *1916*, U. S. Nat. Mus. Proc., vol. 52, p. 394; *1921*, U. S. Nat. Mus. Bull. 112, p. 10.—KEEN, *1937*, West North American Marine Mollusca, p. 23.

Holotype.—U. S. Nat. Museum no. 265905.

Type locality.—Off San Diego, California, in 1090 fathoms, mud; U. S. Bureau of Fisheries "Albatross" Station 5673.

Discussion.—This species has not previously been figured. Photographs of the holotype, supplied by the United States National Museum, show that it is probably a valid *Ennucula* resembling both *N. bellotii* Adams and *N. tenuis* (Montagu). From the former it is distinguished by its less prominent beaks, from the latter by its smaller size, and from both by the fact that the chondrophore though oblique is largely detached from the hinge line. The dimensions given by Dall are: Length, 16; height, 11.5; diameter, 8 mm. No specimens have been available for study.

NUCULA (NUCULA) CAPAYENSIS Schenck, n. sp.
Plate 6, figures 16–18, 20

Holotype.—No. 30196, University of California Museum of Paleontology, Berkeley.

Type locality.—No. A-1319, Capay Valley, Yolo County, California, about 700 feet south and 100 feet west of the east quarter corner of sec. 26, T. 10 N. R. 3 W. M. D. B. & M.

Geologic occurrence.[2]—Capay formation (Eocene), about 600 feet east of the contact between the Eocene and Cretaceous rocks, and stratigraphically about 200–350 feet above the base of the Capay formation, which here totals about 1500–1800 feet.

Description.—Shell large for subgenus; dorsal margin gently convex; anterior extremity bluntly pointed dorsal to the convex ventral margin; posterior side truncate, but slightly inclined, giving a weak rostrate appearance to shell; numerous radial ribs up to about 560μ in width, separated by narrow interspaces; inner ventral margin

[2] Locality and geologic data were furnished by J. M. Kirby, letter dated December 29, 1936.

crenulate; chondrophore oblique; about 12 posterior, 26 anterior teeth; escutcheonal area set off by low sunken area; beaks opisthogyrate; length (dorsal margin horizontal), 32 mm, height, 22.5 mm, semithickness, 6.8 mm, umbonal angle, 115°.

Comparisons.—This species has the general profile and ornamentation of the smaller species, *Nucula* (*Nucula*) *cooperi* Dickerson, 1913, (Calif. Univ., Dept. Geol. Sci., Bull. vol. 7, no. 12 p. 290, pl. 14, figs. 2a, 2b), described from the Eocene of Marysville Buttes, Calif. Although Dickerson's figures are generalized, it is because of mediocre preservation that no chondrophore appears; the shell is broken at its posterior ventral margin; 18 ± anterior and 8 ± posterior teeth on holotype; the flat radial ribs measure about 130 μ in width and are separated by narrow interspaces, as in *Nucula nucleus;* apparently the ribs are not crossed by distinct concentric sculpture, as in the case of *N. vitis* Anderson and Hanna; the escutcheonal area is surrounded by a low, sunken area; the largest specimen of *cooperi* about 12.0 mm in length, is only questionably adult.

It is unwise to suggest close relationships of species from California with those from England, because, as is well known, the English Eocene nuculid pelecypods are in need of revision and better descriptions. Nevertheless, attention is directed to the similarity between *capayensis* and *Nucula bowerbankii* J. Sowerby, 1834, to judge from the protograph and from Wood's (Paleont. Soc. London, vol. 16, pp. 109–110, pl. 18, fig. f, 14, a, b, 1864) figure of a shell presumably from "Haverstock Hill." The type of *bowerbankii* is from the "London clay" found in a well at Lower Heath, Hampstead.[3]

Arthur Wrigley examined, at my request, the type specimen of *Nucula bowerbankii*, no. 69391 in the British Museum (Natural History). He reports (letter dated Jan. 30, 1937) that the holotype corresponds exactly with the figure. Although described as "smooth externally" it is visibly radiated. The specimen figured by Wood is in the same museum, no. 72577, from the London clay of Potters Bar; this specimen is almost identical with the holotype. The specimens of this species come from the middle and lower parts of the London clay; that is, from the second and third divisions of the London clay (Wrigley, 1924, Geol. Assoc. Proc., vol. 35, p. 251). The stage is thus Ypresian, in the restricted sense.

A. G. Davis has kindly given me specimens of *bowerbankii* (Schenck coll. no. 2234). Comparison of these with *capayensis* shows that, except for the rounded rostrum of the latter, the two species are identical in outline; in *bowerbankii* the rostrum is less round and less conspicuous. The radial sculpture of *bowerbankii* is somewhat more pronounced than that of *capayensis* and distinctly finer: on the lateral surface there are approximately two ribs per millimeter for *bowerbankii*, whereas the ribs of *capayensis* average one per millimeter.

Geologic age.—The original definition of the Capay formation is an abstract of a paper by T. H. Crook and J. M. Kirby (Geol. Soc. Am. Proc. for 1934, pp. 334–335, June, 1935). This gives the type locality of the formation as "Capay Valley west of the Rumsey Hills." The fauna is said to be identical with that of the Butte gravels of Marysville Buttes; these gravels were named as a cartographic unit in 1929 by Howel Williams (Calif. Univ., Dept. Geol. Sci., Bull., vol. 18, pp. 112–129). Clark and Vokes (Geol. Soc. Am. Bull., vol. 47, no. 6, pp. 859–860, June, 1936) correlate the "Capay stage" with the Ypresian of western Europe. The similarity between *Nucula capayensis* and *bowerbankii* would not be disharmonious with this suggested synchronization.

NUCULA (NUCULA?) THIELEI
Schenck, new name

Nucula aequalis THIELE, *1931*, in THIELE and JAECKEL, Wissen. Ergeb. d. Deut. Tiefsee-Exp., Bd. 21, Heft 1, p. 199, pl. 6 (2), fig. 46, 46a. *Not* J. DEC. SOWERBY, *1840*, Geol. Soc. London Trans., ser. 2, vol. 5, expl. pl. 39, fig. 3, "Coal-measures," Coalbrooke Dale, Coalfield.

Type material.—University of Berlin; 2 valves.

Type locality.—"Valdivia" station 191: 0° 39.2′ south lattitude, 98° 52.3′ east longi-

[3] The specimen figured as this species by Frauscher (Wien. Ak. Wiss. Denkschr., Nat.-Cl., Bd. 51 (2), p. 135, pl. 7, fig. 6, 1886) may be misidentified.

tude, 750 meters deep; near Siberu Island. Indo-Pacific Province.

Discussion.—The original figures shows no chondrophore, but the original description states that the "Ligamentknorpel klein, zwischen den Zahnreihen gelegen." The inner ventral margin is crenulate. The new name is given in honor of the late Johannes Thiele.

NUCULA (NUCULA) EXIGUA Sowerby, 1833

Plate 6, figures 1–8, 11

Nucula exigua SOWERBY, *1833*, Zool. Soc. London Proc. for 1832, pt. 2, p. 198.—D'ORBIGNY, *1846*, Voyage dans l'Amérique méridionale, Mollusques, vol. 5, part 3, p. 625.—HANLEY, *1860*, in SOWERBY, Thesaurus Conch., vol. 3, p. 154, pl. 229 (N. IV), fig. 136.—?CARPENTER, *1863*, Zool. Soc. London Proc., p. 364.

?*Nucula striata* KING, *1831*, [not Lamarck], Zool. Jour., vol. 5, p. 337.

Type material.—British Museum (Natural History).

Type locality.—"Bay of Caracas," probably a locality on the island of Curaçao, according to H. D. Hedberg (letter dated December 8, 1935).

Discussion.—R. Winckworth has examined the two type specimens of *exigua* in the British Museum (Natural History); he reports (letter dated Feb. 8, 1936) that Hanley's figure in "Thesaurus Conchlyiorum" is an excellent one "for shape and facies" and that under a strong lens *exigua* looks reticulated, though the concentric ribs are actually stronger than the radial decussation. This statement is confirmed by photographs of the types—one entire specimen and two odd valves—subsequently furnished me by the British Museum; these photographs are reproduced in plate 6. The original dimensions given by Sowerby are: "longitude 0.2, latitude 0.1, altitude 0.15 poll." In terms of the metric scale the dimensions would be approximately: length, 5 mm, height, 3.7 mm, thickness, 2.5 mm; the length indicated in Hanley's figure (reproduced on pl. 6, fig. 11) is 4.0 mm. The lengths of twenty specimens from the West Coast of North America in the Stanford Collection range from 3.2 to 5.2 mm, with an average of 4.6 mm.

NUCULA (NUCULA) SUPRASTRIATA Arnold, 1903

Plate 6, figures 9, 10, 12, 13

Nucula (*Nucula*) *suprastriata* "Carpenter" ARNOLD, *1903*, California Acad. Sci., Mem., vol. 3, p. 96, pl. 18, fig. 6.—KEEP, 1904, *West Coast Shells*, 2d ed., p. 20.

Type material.—Holotype apparently lost. Hypotype, Stanford Univ. Paleo. Type Coll. no. 6059.

Type locality.—"Upper San Pedro series, Los Cerritos," i.e., Pleistocene, Signal Hill, Los Angeles County, California. Hypotype from the upper Pleistocene of Upper Potrero Canyon, about ¼ mile south of Pacific Palisades postoffice, Santa Monica, Los Angeles County, California.

Material examined.—Numerous specimens, all virtual topotypes, from the San Pedro Pleistocene (Arnold and T. S. Oldroyd collections); three specimens from Pleistocene at Spanish Bight, San Diego County, California.

Discussion.—As has been pointed out by Grant and Gale (San Diego Soc. Nat. Hist. Mem., vol. 1, p. 111, 1931), Carpenter's use of the name *suprastriata* was apparently only in manuscript; Arnold, therefore, must be regarded as its author, and Arnold's figured specimen becomes holotype. Search among the specimens in the Delos Arnold collection, now at Stanford University, has thus far failed to discover the holotype.

Although most authors have considered this species to be synonymous with *exigua* there are consistent differences which would seem to warrant its recognition as a separate unit. The radial sculpture of *exigua*, as is shown in plate 6, is both stronger and coarser. Most specimens of *suprastriata* show traces of radial sculpture only near the ventral margin; those which are more conspicuously ribbed rarely if ever approach the degree of reticulation seen in the syntypes of *exigua*. Both lunule and escutcheon are more deeply impressed in *suprastriata*, the escutcheon in particular causing a marked break in the contour of the concentric ribs. Although the illustrations of the two species would seem also to indicate differences of outline, this distinction is not constant in a larger suite of specimens. The most convincing difference between the two is in size, *suprastriata* being consistently the

larger. Twenty-five specimens of *suprastriata*, selected at random from a large sample, were found to range between 3.1 and 7.2 mm in length, with an average of 5.8 mm. As has been shown, a similar sample of *exigua* averaged 4.6 mm in length. No specimens of *exigua* were found that exceeded 5.2 mm, while many *suprastriata* reached a length of 7.0. The dimensions cited by Arnold are: length, 5.8, altitude, 5.2, diameter, 3 mm; the specimen which he figured is said to be 7.0 mm in length. The hypotype figured here measures: length, 5.0, height, 4.0, semi-thickness, 1.7 mm. The approximate metric equivalents for *exigua*, according to the original description, would be, length, 5 mm, height, 3.7, thickness, 2.5 mm. The first figure of *exigua* carries a length indication of 4.0 mm, while the photographs published here indicate a length of 4.2 to 4.5. *N. suprastriata* averages, then, from a fifth to a half longer than *N. exigua*.

Distribution.—*Nucula suprastriata* is fairly common in the Pleistocene deposits of southern California. It has not been detected among Recent West American specimens examined, which have all proved to be *exigua*.

SPECIES INADEQUATELY DIAGNOSED

"NUCULA" LEVATIFORME Walcott, 1884

Nucula levatiforme WALCOTT, *1884*,[4] U. S. Geol. Surv. Mon. 8, p. 241, pl. 22, figs. 1, 1a.
Nucula levatiformis Walcott, MILLER, *1889*, North Am. Geol. and Paleo., p. 495.—WELLER, *1898*, U. S. Geol. Surv. Bull. 153, p. 378.

Type material.—U. S. Nat. Mus.

Type locality and age.—Lower horizon of the Carboniferous "group," east slope of a small conical hill on east side of Secret-cañon road, Cañon, Eureka district, Nevada.

Discussion.—This species was not described nor illustrated sufficiently for a generic allocation. The species may be a nuculid, related to *Nuculopsis okawensis* Schenck.

[4] According to the United States Geological Survey (letter dated Feb. 21, 1936), Monograph 8 was "in mss" June 30, 1884, and was delivered some time between that date and March 16, 1885.

NUCULA (NUCULA) "OVATA" Verrill and Bush, 1898

Nucula proxima ovata VERRILL and BUSH, *1898*, U. S. Nat. Mus. Proc., vol. 20, no. 1139, p. 852, pl. 81, fig. 6, pl. 88, fig. 5.—JOHNSON, *1934*, Boston Soc. Nat. Hist. Proc., vol. 40, no. 1, p. 15.
Not Nucula ovata G. P. DESHAYES, *1824*, Description des coquilles des environs de Paris, t. 1, pp. 230, 231, pl. 36, fig. 13, 14.—*Not Nucula ovata* Mant., STOLICZKA, *1871*, Paleontologia Indica, ser. 6, vol. 3, p. 326.

Holotype.—Unknown.

Type locality.—Vineyard Sound, off Cuttyhunk, in 18 fathoms, Atlantic Ocean.

Discussion.—This name is a primary homonym. Requests for specimens were fruitless. Hence no attempt is made to rename the Recent "variety."

In addition to its occurrence at the type locality, Johnson (9) records this nuculid from 440 fathoms off Georges Bank.

"NUCULA LUCIDA Blanding"

Nucula lucida, Blanding. GOULD, *1841*, Report on the invertebrates of Massachusetts, p. 105.
Nucula lucida Gould. CARPENTER, *1863*, Rept. Brit. Assoc., p. 644.—DALL, *1897*, Nat. Hist. Soc. Brit. Col. Bull. 2, p. 6.—*Not* BÖHM, *1891*, Palaeontographica, Bd. 38, p. 76, pl. 3, figs. 20a, b. Cretaceous; doubtfully a nuculid.

The following report is by Dr. H. A. Pilsbry (letter dated Oct. 29, 1935), of the Philadelphia Academy of Sciences:

I believe that "*Nucula lucida* Blanding" of Gould has never been described. Or at least, I had no reference to it, and a search has brought nothing to light. The specimen referred to by Gould has the label "*N. lucida* Gould. Charleston, S. C. Dr. Blanding." It is no. 43381 of the collection; one perfect shell. It differs in outline from *N. tenuis* and is clearly a different species. William Blanding of Columbia, S. C., was elected a corresponding member of the Academy in 1836. He gave specimens from time to time, chiefly vertebrates, birds, etc. I cannot find that he had anything to do with mollusks beyond contributing a few specimens.

NUCULA? BUSHAE G. Dollfuss, 1898, emend. Schenck

Nucula bushi G. DOLLFUSS, *1898*, Revue critique de paléozoologie, no. 4, p. 180. New name for *Nucula subovata* Verrill and Bush (1898) *not* D'Orbigny, *1850*.
Nucula subovata VERRILL and BUSH, *1898*, U. S. Nat. Mus. Proc., vol. 20, no. 1139, p. 852, pl.

81, fig. 8; pl. 83, fig. 5.—JOHNSON, *1934*, Boston Soc. Nat. Hist. Proc., vol. 40, no. 1, p. 15.

Type material.—No. 40474, U. S. Nat. Museum.

Type locality.—444 fms., off Maryland, lat. 37° 59′30″ N., long. 73° 48′40″ W. (U. S. Bureau Fisheries sta. 2171).

Discussion.—This species apparently has a smooth inner margin. Its generic allocation must await examination of the type material. The specific name is emended to *bushae*, since it obviously refers to Katherine J. Bush, coauthor with Verrill.

This nuculid is also present at U. S. Bureau of Fisheries station no. 2249, 53 fms. south of Nantucket, Mass., lat. 40° 11′ N., long. 69° 52′ W., according to data supplied by P. Bartsch.

"NUCULA VENTRICOSA" Pčelincev, 1927

Nucula ventricosa V. PČELINCEV, *1927*, Comité Geol. Leningrad Mém., n. ser., livr. 172, pp. 42 and 61, pl. 1, figs. 30–32. *Not* Sowerby, FLEMING, *1828*, Hist. British Anim., p. 403.—*Not* HINDS, *1843*, Zool. Soc. Proc., pt. 11, p. 100.—*Not* HALL and MEEK, *1855*, Am. Acad. Arts Sci. Mem., n. s., vol. 5, p. 385, pl. 1, figs. 11a, 11b.—*Not* HALL, *1858*, Geol. Survey Iowa, vol. 1, p. 716, pl. 29, figs. 4, 5.

Type locality.—Crimea, near the village of Kučuc-koi; Bathonian and/or upper Bajocian (Jurassic).

Discussion.—In his English summary Pčelincev says this species " . . . differs from *N. variabilis* Sow. by the different character of the convexity of the valves." The original description, in Russian, is not more illuminating, save that it adds that the greatest convexity is just below the beaks. This characteristic is hardly sufficient for differentiation of nuculid species. The illustrations given are too poor to make possible a decision as to the validity of the species. Although the name *ventricosa* is many times a homonym, renaming the species without well-preserved material at hand would serve no useful purpose. It is safe to say, however, that the species is not *Nucula, sensu stricto.*

"NUCULA (NUCULA) SULCATA Bronn, 1831"

Nucula sulcata BRONN, *1831*, Ergeb. nat. Reisen, II, p. 617 (fide SHERBORN, Index. Anim., *1931*, ser. 2, part 25, p. 6305).—*Not* HISINGER, *1841*, Leth. Suec., Suppl. Secund. Contin., p. 3 (fide SHERBORN, *1931*, Index Anim., *supra cit.*, p. 6305).—*Not* A. ADAMS, *1856*, Zool. Soc. London Proc., pt. 24, p. 53.—HANLEY, *1860* in SOWERBY, Thes. Conch., vol. 3, p. 153, pl. 229, fig. 127.

Since a thorough search in several of the larger libraries in America failed to produce a copy of Bronn's work, *N. sulcata* Bronn cannot be discussed. Recent specimens from the west coast of Sweden identified as this species are related to *N. nucleus.*

Adams' *sulcata* has New Zealand as its type locality. Since the original description states that the valves are radially striate and the ventral margin crenulate, the species belongs to *Nucula, s.s.*

NUCULA "DONACIFORMIS" Harder, 1913

Nucula donaciformis HARDER, *1913*, Danmarks geologiske Undersøgelse, II. Raekke, Nr. 22, p. 49, 50, 121, 122, pl. 3, figs. 10, 11.—*Not* SMITH, *1895*, Ann. and Mag. Nat. Hist., ser. 6, vol. 16, p. 15, pl. 2, fig. 8.—*Not* PRASHAD, *1933*, Archiv. f. Naturgeschichte, n. f., Bd. 2, Heft 1, p. 128, pl. 1, fig. 4.

Not *Nucula? donaciformis* HALL, *1847*, Palaeont. New York, vol. I, p. 316, pl. 33, fig. 3a, 3b.

The species from the upper Oligocene of Aarhus, Jutland, Denmark, may comprise a biological unit worthy of a separate name, and it is hoped that the Danish geologists will rename the species if such action is justified.

NUCULA "CANCELLATA" Vredenburg, 1928

Nucula cancellata Vredenburg, *1928*, Geol. Surv. India Mem., vol. 50, pt. 2, p. 420, pl. 33, figs. 4, 8, 10–13.—*Not* MEEK and HAYDEN, *1856*, Acad. Nat. Sci. Philadelphia Proc., vol. 8, p. 85, 285 (see p. 27).—*Not* JEFFREYS, *1881*, Zool. Soc. London Proc., p. 951 (see *N. atacellana* Schenck, p. 27).

Type locality.—Gáj (Miocene) of Kachh, northwest India.

Discussion.—This species resembles *Nucula rugosa* Odhner, 1919, (Arkiv f. Zool. K. Svenska Vetenskap., bd. 12, no. 6), p. 23, pl. 2, figs. 15–18), from Madagascar, Recent, differing in the following respects: the radial sculpture is stronger in *cancellata*, being reflected on the interior of the shell by heavier crenulations; *rugosa* is more tumid in outline, with a deeper, more protruding escutcheon; both anterior and posterior rows of hinge teeth are more nu-

merous in *rugosa*, averaging 23 and 9, respectively, as contrasted to 15 and 8 in *cancellata*. Vredenburg compares his species to *N. studeri* d'Archiac and *N. rugulosa* Sowerby; the latter is discussed in this paper. No specimens being available for study, the homonym is not renamed here.

Family Nuculanidae
Cyrilla munita (Dall), 1898
Plate 6, figures 14, 15

Pleurodon (*Cyrilla*) *munita* "Carpenter." Dall, *1898*, Wagner Free Inst. Sci. Trans., vol. 3, pt. 4, p. 602; *1921*, U. S. Nat. Mus. Bull. 112, p. 14.

Nucinella munita [Dall]. Keen, *1937*, West North American Marine Mollusca, p. 23 (also on p. 20 under *Cyrilla*).

Nucula petriola Dall, *1916*, U. S. Nat. Museum Proc., vol. 52, p. 395; *1921*, U. S. Nat. Mus. Bull. 112, p. 10.

Type material:—Holotype of *munita*, U. S. National Museum (?); of *petriola*, U. S. National Museum, no. 271416.

Type locality:—Of *munita*, Catalina Island, California; of *petriola*, off Santa Rosa Island, California, in 53 fathoms, mud.

Discussion.—Harald A. Rehder, of the United States National Museum, informs me that *Nucula petriola* Dall is undoubtedly "*Pleurodon*" *munita*. Photographs of the holotype confirm his decision. Unfortunately, *Pleurodon* is a homonym unavailable for the Mollusca. Two generic names are candidates for substitution—*Nucinella* Wood, 1850 (genotype, *N. miliaris* (Deshayes), from the Eocene of the Paris Basin) and *Cyrilla* A. Adams, 1860 (genotype, *Huxleyia sulcata* A. Adams, 1860, a recent Japanese species). Pending a taxonomic study to show whether or not *Cyrilla* is subordinate to *Nucinella*, *Cyrilla* is tentatively used here in a generic sense.

As the West American species has never, apparently, been figured, the illustrations of *petriola* are included here.

PREPARATION FOR THE "FOSSILIUM CATALOGUS"

In 1934, I optimistically undertook to prepare a catalogue of species of Nuculidae for the "Fossilium Catalogus." I began by an attempt to examine types and topotypes of the various species, in the hope of weeding out the numerous mistakes that have crept into the literature. I planned also to consult the original descriptions of all the species. The present paper illustrates a few of the difficulties encountered. It is evident that a thoroughgoing review of the thousand-odd candidate species of the Nuculidae must be a work of many years. The allocations suggested in the following pages constitute, therefore, only a beginning, an inventory of the nuculid species for which specimens have been available or which have been adequately figured. Much more study material will be needed before the synonymies of many of the species can be determined.

PRELIMINARY GENERIC AND SUBGENERIC ALLOCATION OF SPECIES

Genus Nucula Lamarck, 1799
Subgenus *Nucula, sensu stricto*

Type, *Arca nucleus* Linné.

atacellana Schenck
aturensis Cossmann and Peyrot
benoisti Cossmann and Peyrot
broni Deshayes
bruxellensis Gilbert
callicredemna
capayensis Schenck
castanea Adams
compressa Phillippi
comta Goldfuss
consors Wood
cooperi Dickerson
cossmanni E. Vincent
decussata Sowerby
degrangei Cossmann and Peyrot
duchastellii Nyst
exigua Sowerby
gaultina Gardner
groenlandica Posselt
haesendoncki Nyst
hanleyi Winckworth
hartvigiana Pfeiffer
headonensis Morris
jeffreysi Bellardi
lattorfiana Schenck
lunulata Nyst
magnifica Conrad
marshalli Schenck
mayeri Hoernes
mixta Deshayes
nitidosa Winckworth
nucleus Linné
oligodonta Cossmann and Peyrot
papillifera Thiele
parisiensis Deshayes
proxima Say
regnorum Wrigley
rugosa Odhner
rugulosa Sowerby
sagittata Suter
sculpturata Sowerby
similis Sowerby
somaliensis Thiele
sulcata Bronn
?sultana Thiele
sumatrana Thiele
sunaria Dall
suprastriata Arnold
taphria Dall
thanatiana Wood
truncula Dall
tumidula Malm
turgida Marshall
vitis Anderson and Hanna
waltonia Gardner

Subgenus Pectinucula Quenstedt, 1930

Type, *N. pectinata* Sowerby.

cancellata Meek and Hayden
bidorsata Stoliczka
crassicula Stoliczka
luciae Seguenza
notabilis Mayer
pectinata Sowerby
piligera Sandberger
radiatocostata Nagao
subredempta Böhm
tenera Müller
truncata Nilsson

Subgenus ENNUCULA Iredale, 1931

Type, *Nucula obliqua* Lamarck.

bellotii Adams
delphinodonta Mighels
obliqua Lamarck
niponica E. A. Smith
profundorum E. A. Smith
puelcha D'Orbigny
tenuis Montagu

Subgenus LINUCULA Marwick, 1931

Type, *Nucula ruatakiensis* Marwick.

ruatakiensis Marwick
?sultana Thiele
tutamoensis Marwick
waipaoa Marwick

Genus ACILA H. and A. Adams, 1858

Consult Schenck, Special Paper no. 4, Geol. Soc. America, 1936, but add

kurodai Kanehara
osawaensis Nomura and Zinbô
yanagawaensis Nomura and Zinbô

Genus PRONUCULA Hedley

Type, *P. decorosa* Hedley.

concentrica Cotton
decorosa Hedley
flindersi Cotton
hedleyi Pritchard and Gatliff
micans Angas
totagiensis Marwick

Genus NUCULOMA Cossmann, 1907

Type, *Nucula castor* D'Orbigny.

castor D'Orbigny

Genus NUCULOPSIS Girty, 1911

Type, *Nucula girtyi* Schenck, n.n. for *Nucula ventricosa* Hall.

Subgenus NUCULOPSIS, *sensu stricto*

girtyi Schenck
gibbosa Fleming
tateiana King

Subgenus PALAEONUCULA Quenstedt, 1930

Type, *Nucula hammeri* Defrance.

croneisi Schenck
hammeri Defrance
levatiforme Walcott
okawensis Schenck
pulchella Beede and Rogers
strigilata Goldfuss
welleri Schenck
wewokana Girty
yuani Chao

Genus BREVINUCULA Thiele, 1934

Type, *Nucula guineensis* Thiele.

guineensis Thiele
verrillii Dall

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A PRELIMINARY REVIEW OF CERTAIN FAMILIES OF DIPTERA FROM THE FLORISSANT MIOCENE BEDS. II.

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ABSTRACT—The fossil Asilidae of the Florissant Miocene are discussed, and six new species are described. Complete keys and some critical notes are given. The Bibionidae, Stratiomyidae, Empididae, and Asilidae have not undergone much evolutionary development since the Miocene. The Florissant fauna in the families indicates a warm, humid climate, but not a tropical one.

IN A PREVIOUS paper (James, 1937) I reviewed the dipterous families Bibionidae, Stratiomyidae, and Empididae as they are known to have occurred in the Miocene of Florissant. The present paper deals with the Asilidae, or robber flies, of the same beds. Its purpose is to summarize the work that has been done on this family, but without any pretense of a comprehensive critical review, which would presuppose intensive work on some as yet poorly understood morphological characters of living forms. Types of the new species, unless otherwise stated, are in the University of Colorado Museum.

Family ASILIDAE

The Asilidae formed an important element in the Florissant insect fauna. The species that have been preserved as fossils are related to living ones, all being referred, though in some cases not without question, to extant genera. In the study of the fossil Asilidae, unfortunately, too much reliance must be placed upon wing venation, since the terminalia, chaetotaxy, and antennae, all quite valuable in the taxonomy of recent species, are not well enough preserved, as a rule, to be used in the study of the fossil forms.

Of the four subfamilies, the Laphriinae have not yet been recorded from these beds, while the Leptogastrinae are known only from one unnamed species recorded by Cockerell (Entomologist, 1913: 214). The Leptogastrinae may readily be recognized by their very slender form, the lack of an alula, and the broadly open anal cell; the discal cell is low on the wing, much nearer the posterior than the anterior margin, and is often distant from the apex, the submarginal and posterior cells, consequently, being long. The Asilinae and Dasypogoninae are most robust, with well developed alulae, and with the anal cell closed or narrowly open; in the Asilinae the marginal cell is closed and petiolate, whereas in the Dasypogoninae it is open.

The following key, based upon the original descriptions and a study of the types in the University of Colorado Museum, will separate the known species of the Florissant Miocene.

KEY TO THE FLORISSANT ASILIDAE

1. Marginal cell closed and petiolate 2
   Marginal cell broadly open 7
2. The second submarginal cell twice as wide at the apex as in the middle, the apical width resulting from the strong bend in vein R_5 beyond its middle..... .....*Senoprosopis antiquus*
   The second submarginal cell not more than one and one-half times as wide at the apex as in the middle, the vein R_5 not being strongly bent downward..... 3
3. Cross-vein r-m definitely beyond the middle of the discal cell 4
   Cross-vein r-m at or but slightly beyond the middle of the discal cell; the sides of the second submarginal cell amost parallel on the basal half..... 6
4. Marginal cell very narrow; its apex sharply pointed, its lower vein scarcely or not at all bowed at the apex..*Asilus peritulus*
   Marginal cell broader and less pointed, the lower nervure more or less bowed..... 5
5. The fourth posterior cell with a short petiole at its base; the first posterior cell strongly constricted in the middle, at which point its width is less than that of the base of the second posterior cell.....*Philonicus saxorum*
   The fourth posterior cell sessile and separated from the second basal by a short

cross-vein; the base of the second posterior cell narrower than the narrowest part of the first posterior..... .....*Asilus amelanchieris*

6. The fourth posterior cell not petiolate at the base; bristles and hairs pale, not evident except under a compound microscope.....*Asilus wickhami*
   The fourth posterior cell short-petiolate; legs with conspicuous bristles..... .....*Asilus florissantinus*
7. Fourth posterior cell closed..... 8
   Fourth posterior cell open.....12
8. Very large flies, 30–40 mm in length; union of second posterior and discal cells punctate..... 9
   Medium-sized flies, 20 mm or less in length; union of second posterior and discal cells broad.....10
9. Anal cell narrowly open; height of marginal and first submarginal cells at cross-vein r-m definitely greater than the cross-vein.....*Microstylum? destructum*
   Anal cell closed; marginal and first submarginal cells at cross-vein r-m no higher than the cross-vein..... .....*Microstylum wheeleri*
10. The side of the discal cell bordering the second posterior cell twice as long as the side bordering the third posterior..... .....*Saropogon oblitescens*
    The side of the discal cell bordering the third posterior cell longer than that bordering the second.....11
11. Vein R_4 forming approximately a 60° angle at its union with R_5; R_4 ending slightly beyond the wing apex; first posterior cell definitely narrowed at its apex .....*Senobasis borealis*
    Vein R_4 meeting R_5 at an angle of about 30°; R_4 ending before the wing apex; first posterior cell not narrowed apically .....*Lestomyia miocenica*
12. Cross-vein r-m distant from the base of the second submarginal cell by approximately the length of that cell.....13
    Cross-vein r-m not nearly so far from the base of the second submarginal cell as the length of that cell.....14
13. Larger species (type, 10.7 mm)..... .....*Dioctria pulveris*
    Smaller species (type, 8 mm)..... .....*Dioctria florissantina*
14. Very hairy, robust species; antennae considerably longer than the head; furcation of R_5 remote from discal cell..... .....*Ceraturgopsis praecursor*
    Less robust, only moderately hairy species; antennae no longer than head.....15
15. Second submarginal cell about 2.5 mm long; anal cell open...*Nicocles miocenicus*
    Second submarginal cell less than 2 mm long.....16
16. Vein between discal and second posterior cells as long or longer than that between discal and third posterior cells; furcation of R_5 near apex of discal cell.....17
    Vein between discal and second posterior cells much shorter than that between discal and third posterior cells; furcation of R_5 remote from apex of discal cell.. .....*Taracticus renovatus*
17. Venation very pale; second submarginal cell comparatively broad (0.3 mm at 0.5 mm from apex); sides of discal cell at apex equal.....*Cophura antiquella*
    Venation dark; second submarginal cell very narrow (0.3 mm at 0.25 mm from apex); sides of discal cell at apex unequal, the upper being the longer..... .....*Taracticus contusus*

Genus SENOPROSOPIS Macquart, 1838

SENOPROSOPIS ANTIQUUS, James, n. sp.
Text figure 2

Female.—Length, 24 mm; of wing, 13 mm; of head, 2 mm; of thorax, 5 mm; of abdomen, 17 mm; width of wing, 4 mm. Antennae missing. Body color evidently brownish. Legs robust, thickly clothed with black pile, set with heavy bristles, which vary in color from brown to black; the tarsi especially bristly. Wings hyaline, with brownish veins; the marginal, fourth posterior, and anal cells closed and petiolate; the sides of the second submarginal cell approximately parallel on its basal half, but flaring at its apex, the apex of the cell being about twice as broad as its middle. The following measurements are in millimeters: petiole of marginal cell, 0.6; maximum width of marginal cell, 0.6; length of second submarginal, 4.5; width at center, 0.5, at apex, 1.0; cross-vein r-m, 0.4; length of discal cell, 3.7; base of discal cell to cross-vein r-m, 2.3; cross-vein r-m to apex of discal cell, 1.4; discal cell on second posterior, 0.3, on third posterior, 0.6, on fourth posterior, 2.4; length and greatest width of fourth posterior cell, 3.0 and 1.0 respectively.

Type: Holotype, Miocene shales of Florissant. An excellently preserved specimen, lying on the side. University of Michigan Museum, no. 12160.

The generic reference is made on the basis of the figure of the wing of *Senoprosopis* in Curran's North American Diptera, page 137. In Curran's illustration, the marginal cell is more obtuse at the apex, the cross-vein r-m joins the discal cell approximately at its center, and the fourth posterior cell is not as broad. The general form of

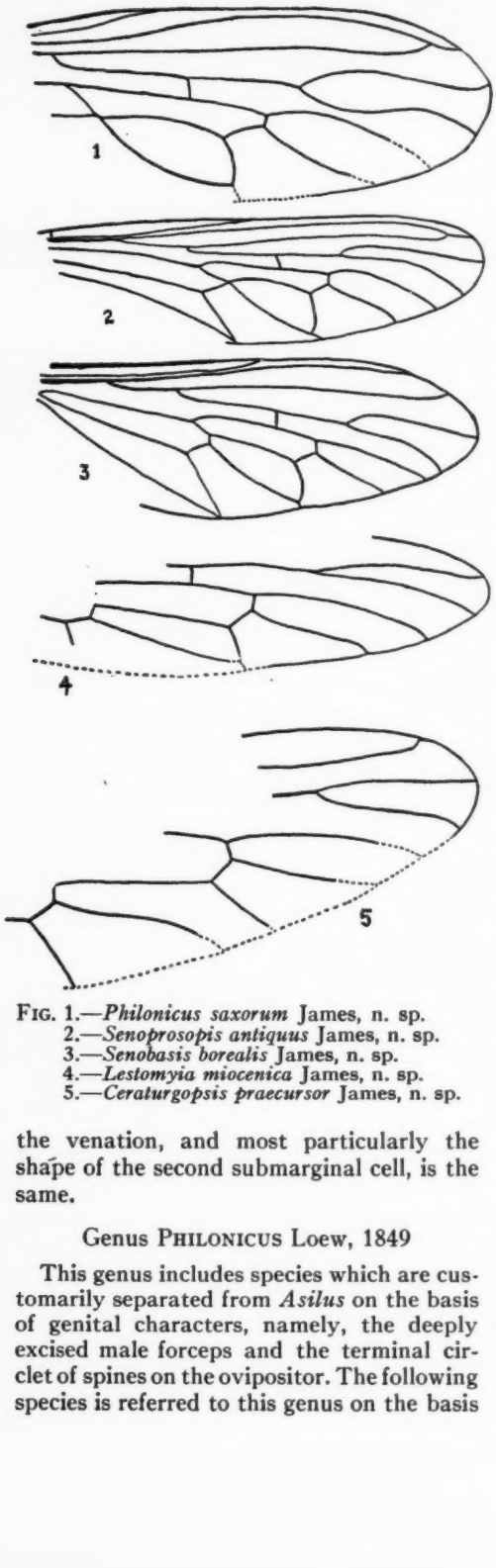

FIG. 1.—*Philonicus saxorum* James, n. sp.
2.—*Senoprosopis antiquus* James, n. sp.
3.—*Senobasis borealis* James, n. sp.
4.—*Lestomyia miocenica* James, n. sp.
5.—*Ceraturgopsis praecursor* James, n. sp.

the venation, and most particularly the shape of the second submarginal cell, is the same.

Genus PHILONICUS Loew, 1849

This genus includes species which are customarily separated from *Asilus* on the basis of genital characters, namely, the deeply excised male forceps and the terminal circlet of spines on the ovipositor. The following species is referred to this genus on the basis of the similarity of its venation to that of the living *P. limpidipennis* Hine.

PHILONICUS SAXORUM James, n. sp.
Figure 1

Female.—Length of abdomen, 9.5 mm, of wing from origin of R_{4+5} to apex, 5.5 mm; probable entire length of wing, about 10 mm. The wing venation and shape of the abdomen make the generic reference fairly certain, the ovipositor is cylindrical, but I can not be certain of the terminal spines. The wing differs from that of the recent *P. limpidipennis* chiefly in the much greater narrowing of the first posterior cell at its middle and the correspondingly greater bulge (outward) of veins R_5 and M_1.

Thorax black, clothed with black hairs and bristles; abdomen reddish, paler ventrally, the seventh segment and ovipositor black; some black hair dorsally on abdominal segments 4, 5, 6, and 7, denser on the posterior segments. Legs probably largely pale, but poorly preserved. Wings apparently yellowish hyaline, the veins clear yellow; marginal cell narrow at apex; veins R_4 and R_5, particularly the latter, with strong double curves, thus decidedly narrowing the second submarginal cell medially; veins R_5 and M_1 closely approaching each other, thus making the first posterior cell very narrow medially and greatly expanded apically; cross-vein r-m at about two-thirds the length of the discal cell, slightly oblique; the discal cell touching the fifth posterior cell for a short distance, the cross-vein m-cu being eliminated.

Holotype: Miocene shales of Florissant, station 14 (W. P. Cockerell).

Genus ASILUS Linnaeus, 1758

ASILUS FLORISSANTINUS James, n. sp.

Male.—Length, exclusive of head, which is missing, 14.5 mm; of wing, 8.5 mm. Thorax black, with reddish hair and bristles; legs yellow, the hind femora brown above; legs copiously clothed with pale hair, the bristles also pale; the hind tibiae with two bristles on the anterior side of each. Wings pale yellow, the veins darker yellow; fourth posterior cell petiolate basally, the mediocubital cross-vein wanting; radiomedial

cross-vein oblique, reaching the discal cell at approximately its middle; sides of second submarginal cell parallel until very near its apex. Marginal cell as in *A. notatus*. Abdomen reddish, darker at the base; the pleura paler; vestiture consisting of pale hair, which increases in length toward the apex of the abdomen; genitalia pale red, clothed with long, reddish pile.

Measurements, in millimeters: length of upper male forceps, 1.3; greatest height of marginal cell, 0.35; height of submarginal cell at center, 0.4; cross-vein r-m to base of discal cell, 1.1; cross-vein r-m to apex of discal cell, above, 1.1; petiole at base of fourth posterior cell, 0.1; greatest height of fourth posterior cell, 0.7; length of fourth posterior cell, 1.7.

Types: Holotype and reverse of type, Miocene shales of Florissant, station 14 (W. P. Cockerell).

ASILUS PERITULUS Cockerell

Asilus peritulus COCKERELL, *1909*, Am. Mus. Nat. History, Bull., vol. 26, p. 69.

In this species, the marginal cell is very narrow and runs to a sharply pointed apex, the vein bounding it on the lower side (R_{2+3}) running in almost a straight line, with hardly any bend apically. This character seems to be well marked, and distinguishes this species from the other Florissant *Asilus*. The second submarginal cell is, as Cockerell described it, very long (about twice as long as the section of vein R_{4+5} from cross-vein r-m to its furcation).

Four specimens in the Museum of Comparative Zoology seem to belong to this species. In one of these, no. 6407, the head is well preserved. The mystax is black and especially dense; the third antennal segment, except for its arista, is well preserved; its length, excluding the arista, is equal to the combined lengths of the first and second segment; its width is about two-fifths its length. Other specimens in the Museum of Comparative Zoology bear the numbers 11804, 1528, and 11814.

ASILUS AMELANCHIERIS Cockerell

Asilus amelanchieris COCKERELL, *1911*, Am. Mus. Nat. Hist., Bull., vol. 30, p. 79.

Cockerell's description characterizes this species sufficiently. It is a black species, with somewhat paler legs, related to the living *Asilus notatus*. The type in the University of Colorado Museum is lying on the side; one wing is completely preserved but is rather fragile. I refer two specimens in the Museum of Comparative Zoology to this species. No. 4899, a male, is well preserved with both wings spread. Its measurements vary somewhat from those of the type, the second submarginal cell being somewhat longer and the cross-vein r-m not so far distant from the center of the discal cell, but still decidedly beyond the center (ratio 22:17 as compared to 24:15 in the type); however, these variations are within the range to be found in living species. No. 2868, a female, more closely approaches the type in its measurements.

ASILUS WICKHAMI Cockerell

Asilus wickhami COCKERELL, *1914*, Acad. Nat. Sci. Philadelphia, Proc., p. 648.

I have seen only the type, which is in the University of Colorado Museum. It is lying on the side. The apex of the abdomen is missing, but the rather robust form suggests a female. The venation is clear, except at the apex toward the posterior side. It is clearly an *Asilus*.

Genus SENOBASIS Macquart, 1838

SENOBASIS BOREALIS, James, n. sp.
Figure 3

Female.—Length, 14.5 mm, of wing 8.5 mm. Head black. Proboscis strong, at least 1 mm in length. Antennae missing. Thorax black, relatively bare and without obvious pilosity; legs yellowish, the tarsi somewhat darker, especially apically, the anterior and middle femora at their apices and the posterior ones on the upper side evidently black. Legs uniformly clothed with rather thick, short pile, but the bristles evident only at the apices of the tibiae and on the tarsi, and in those places rather weak. The anterior tibia terminates in a short but strong spur. Wings hyaline. Fourth posterior cell closed and petiolate at the apex; anal cell closed in the wing margin, its sides straight and its apex strongly angular. The cross-vein r-m joins the discal cell at two-thirds the length of that cell. The following measurements are in millimeters: origin of R_s to separation of R_{2+3} and R_{4+5}, 1.2; origin

of R_{4+5} to r-m, 2.0; r-m to separation of R_4 and R_5, 1.1; length of second submarginal cell, 2.5; of cross-vein r-m, 0.3; contact of discal with second posterior, 0.2, with third posterior, 0.45; cross-vein m-cu, 0.1. Abdomen yellow or light brown, the first segment and the basal half of each of the subsequent ones, however, black; the abdomen somewhat spatulate in outline, narrower at the base, where it measures 2 mm, widest on the fourth and fifth segments (2.5 mm), and from that point gradually tapering to the apex; the genitalia ending in a circlet of spines, at least 4 or 5 on each side.

Holotype: Miocene shales of Florissant, no. 13277. Museum of Comparative Zoology, type No. 4498. A well preserved specimen, lying with the dorsal side exposed, the legs and wings expanded, and practically the complete venation visible in both wings.

The generic reference seems to be satisfactory. The venation shows no important variations from that of *S. mendax* Curran (see Curran, North American Diptera, p. 180, fig. 138), and other characters, so far as visible, are compatible with the generic diagnoses given by Macquart, Williston, and Curran. The abdomen is not as strongly narrowed basally as in some recent forms, but this is a character which might easily be subject to considerable variation.

Genus DIOCTRIA Meigen, 1803

DIOCTRIA FLORISSANTINA (Cockerell)

Leptis florissantina COCKERELL, *1909*, Am. Jour. Sci., vol. 27, p. 58.

Dioctria? florissantina (COCKERELL), *1909*, Ent. Soc. America, Annals, vol. 2, p. 254.

The generic reference to *Dioctria* seems quite satisfactory. The lack of bristles is probably only apparent; the pale, rather weak, bristles of such living species as *D. baumhaueri* Macquart, would be hard to see in a fossilized specimen. The antennae are certainly not of the leptine type; they are strongly suggestive of *Dioctria*, though slightly shorter than in recent species known to me.

Genus CERATURGOPSIS Johnson, 1903

CERATURGOPSIS PRAECURSOR James, n. sp.

Figure 5

Male?—Length of body, 12 mm; of wing, 7 mm, of antennae, 2 mm. Head black, the face apparently prominent, densely clothed with long, reddish hair, which extends also over the cheeks and occiput; antennae twice as long as the diameter of the head, black, paler basally, the basal segments rather indistinct; the terminal segment about 0.4 mm long, triangular, twice as long as wide. Thorax, including legs, black, with dense, long reddish hair; structurally, the legs are typical of *Ceraturgopsis*. Wings, as far as visible, as in recent species; vein R_{4+5}, however, branches at a considerable distance beyond the apex of the discal cell ($1\frac{2}{3}$ times the maximum diameter of the discal cell); the posterior cells are, therefore, correspondingly long. Abdomen densely clothed with long reddish pile on all segments ventrally and on the terminal ones dorsally, that on the dorsum apparently forming dense lateral tufts.

Types: Holotype and reverse of type, Miocene shales of Florissant, station 13B (W. P. Cockerell).

Of recent genera, this species comes closest to *Ceraturgopsis*, and I feel that it should be placed there; however, if the hairiness of the body and the venational anomalies should be considered of sufficient value, it might be referred to an extinct genus. The antennae are typical of *Ceraturgopsis*.

Genus LESTOMYIA Williston, 1883

LESTOMYIA MIOCENICA James, n. sp.

Figure 4

Male.—Length of wing, 5.5. mm, of abdomen 6.5 mm. Head and anterior part of thorax missing; the thorax humped, black, brownish on the pleura; dorsum abundantly supplied with black bristles and coarse hair; pleuron with a tuft of twelve or more trichostical bristles. Posterior legs brown, the femora black above and apically, the tibiae black at their narrow bases and apices; femora without evident bristles; tibiae with abundant short black hairs, six or more black bristles below, at least one subapical above, and several apical ones; tarsi abundantly provided with black hairs and bristles. Wings narrow, venation of the *Lestomyia* type, but the origin of R_{2+3} is far beyond the apex of the discal cell, the portion of the R_s from the cross-vein to the furcation being twice as long as the part of the discal cell touching the first posterior;

consequently, the first, second, and third posterior cells are unusually long. Veins brown. Abdominal segments black basally, brown apically and on venter, the extreme apices yellow. Genitalia small.

Measurements, in millimeters: cross-vein r-m, 0.2; cross-vein to branch of R_s, 1.2; R_{2+3}, 1.6; R_{4+5}, 1.6; contact of discal cell with first posterior, 0.6, with second posterior, 0.15, with third posterior, 0.3, with fourth posterior, 1.2; M_{1+2} from discal cell, 1.6; M_3 from discal cell, 1.2.

Holotype: Male, Miocene shales of Florissant, station 14 (W. P. Cockerell).

The generic reference seems satisfactory. The general appearance of the fly, the contour and structure of the thorax, the bristles of the legs, the narrow wings, and, with the exceptions noted, the venation, agree quite well with *L. sabulonum* and still better with an as yet unnamed species from Arizona.

The following Asilidae have also been described from the Florissant shales:

Microstylum wheeleri Cockerell, *1908*, Canadian Entomologist, vol. 40, p. 173, pl. 4; *1909*, Ent. Soc. America, Annals, vol. 2, pl. 28, fig. 2, Type, University of Colorado Museum.

Microstylum? destructum Cockerell, *1909*, Ent. Soc. America, Annals, vol. 2, p. 254. pl. 28, fig. 2. Type, University of Colorado Museum.

Saropogon oblitescens Cockerell, *1914*, Canadian Entomologist, vol. 46, p. 102. Type, University of Colorado Museum.

Dioctria pulveris Cockerell, *1917*, U. S. Nat. Mus., Proc., vol. 53, p. 392. Type, U. S. Nat. Mus.

Nicocles miocenicus Cockerell, *1909*, Ent. Soc. America, Annals, vol. 2, p. 255, Type, University of Colorado Museum.

Taracticus contusus Cockerell, *1910*, Am. Mus. Nat. Hist., Bull., vol. 28, p. 282. Type, University of Colorado Museum.

Taracticus renovatus Cockerell, *1911*, Am. Mus. Nat. Hist., Bull., vol. 30, p. 80. Type, University of Colorado Museum.

Cophura antiquella Cockerell, *1913*, Entomologist, p. 213. Type, University of Colorado Museum.

GENERAL DISCUSSION

Bequaert and Carpenter (1936) have shown that there is a remarkable similarity between the Miocene and the living Nemestrinidae. The same conclusion may be drawn in regard to the Bibionidae, Stratiomyidae, Empididae, and Asilidae, though in each case, just as in the Nemestrinidae, the Miocene fauna indicates a much warmer climate than that of Colorado today. It was probably subtropical, rather than tropical, however, as indicated by the blending in the fauna of temperate and tropical elements.

Three genera of Bibionidae were recorded in my previous paper: *Plecia*, *Bibiodes*, and *Bibio*, with 4, 1, and 4 species respectively. These figures by no means represent the relative importance of these genera, however; of 150 specimens that I have seen, 11 belong to *Plecia*, 20 to *Bibiodes* and 119 to *Bibio*. About 80 per cent of the *Bibio*, or 65–70 per cent of the Bibionidae, are referred positively or probably to *B. wickhami* Cockerell, which, as I have shown in my previous paper (p. 242), is very close to *B. albipennis*, by far the most common living species throughout most of its range.

Today, *Bibio* is primarily a holarctic genus, with a small representation in the tropics, while *Plecia* is a tropical, particularly neotropical, genus, with a small representation in temperate regions. *Bibiodes* occurs only in the Southwestern United States, so far as is known. Of the three genera, *Plecia* (*Penthetria*) seems to be phylogenetically the oldest (Handlirsch, 1910, p. 95), while *Bibiodes* seems to be a comparatively recent offshoot of *Bibio*.

The Stratiomyidae of the Florissant Miocene show more distinctly tropical affinities. Five genera are known, each represented by one species, and each species unknown except for the types. *Cyphomyia* is today predominantly neotropical, and *Rhingiopsis* exclusively so; both genera are unknown in the temperate regions of the world. *Beris* and *Lasiopa* occur both in the temperate and tropical regions and *Oxycera* is predominantly holarctic.

The Empididae are all of the Empidine type and represent a fauna that might well occur in Colorado today.

The Asilidae are all referred to living genera. Two of these—*Senoprosopis* and *Senobasis*—are today tropical, and *Microstylum* and *Ceraturgopsis*, when found in the temperate regions, occur only in their warmer parts. The strong development of *Asilus* is characteristic of temperate regions today. The absence of such prominent living genera as *Erax*, *Proctacanthus*, *Diogmites*, *Stenopogon*, and *Cyrtopogon* does not necessarily mean that these genera have evolved

since the Miocene, but merely that the habitat at the time may not have been suitable for their occurrence. *Cyrtopogon* today is characteristic of coniferous forests and probably was not adapted to the mixed coniferous and deciduous forests of the Florissant Miocene, whereas the other four genera are characteristic of dry regions, such as arid or desert grasslands.

A consideration of the four families discussed above seems to indicate: (1) that the climate of Florissant in the Miocene was, as has been supposed, considerably warmer than at present, and probably subtropical; (2) that it was more humid than today, probably similar to that of the Gulf States; and (3) that no evolutionary changes of importance have taken place in these families since the Miocene, though the changes between the Eocene and Miocene (as shown by the Green River, Tulameen River, and other such deposits) were marked. Against the second conclusion, we have that of Bequaert and Carpenter, that the climate was dry, and not unlike that of the Southwestern United States today. Though it is hard to explain the occurrence of five species of Nemestrinidae in a humid climate, it would be more difficult to explain an abundance of Bibionidae and Empididae, not to mention the rich mesophytic and hydrophytic vegetation, in a warm, arid region. As a probable solution of this difficulty, I might suggest that we are inclined to forget the temporal aspect of the problem. A study of the stratigraphy of the Florissant shales might show that the climate was not uniform during the duration of the deposits. An alternate, but less probable, explanation is that the lake lay in an arid region, but with a broad zone of mesophytic vegetation, which produced a local climate, around it.

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ERRATUM

In my previous paper, p. 244, fig. 3, the basal part of the radial sector was erroneously labelled "m-cu."

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PNEUMATOCYSTS ON MONOGRAPTUS (LINOGRAPTUS) PHILLIPSI MULTIRAMOSUS

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ABSTRACT—The attachment of the stipes to a central ringlike disc in the first specimen of *Linograptus phillipsi multiramosus* found in the Henryhouse shale along Cool Creek, Oklahoma, suggested the presence of a pneumatocyst on the synrhabdosome. In collections secured later from the same horizon and locality, several specimens of this variety show the same arrangement of the rhabdosomes radiating from a central membranous disc, large parts of which are preserved on several forms. It is purposed to review briefly the evidence of floats on graptolites and to illustrate and describe briefly the pneumatocysts on this relatively new variety.

MOST OF the great number of graptolites preserved in the rocks occur as separate rhabdosomes or stipes. Very few are associated in synrhabdosomes or compound colonies. In the Dendroidea, profuse branching is characteristic. Among the Graptoloidea, some genera are characteristically branched, although these branched types are relatively few as compared to the extremely large number of separate rhabdosomes. In view of the great preponderance of individual rhabdosomes, it seems almost incredible that the floating habit should have been limited to those associated in synrhabdosomes provided with floats. One also wonders if the initial siculae of the rhabdosomes may not have had the power of attaching themselves to any floating object on the surface of the ocean. However, if the floating habit was attained most largely by association into synrhabdosomes with pneumatocysts, that association must have been an extremely loose one, from which the rhabdosomes were easily separated. Accordingly, interest centers keenly about any of the forms found associated in synrhabdosomes.

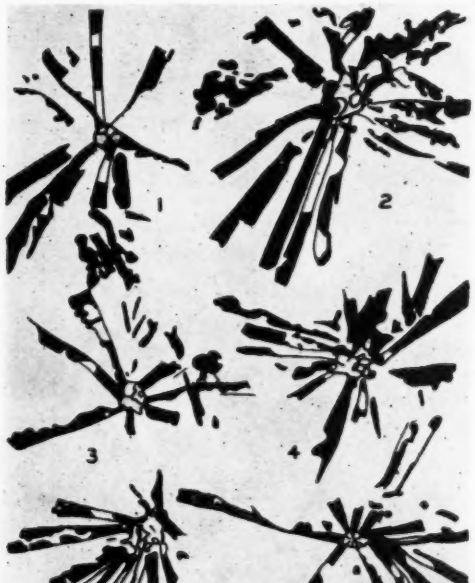
In the Graptoloidea, among the branching types of *Axonophora* (forms with a virgula), Hall (1) recognized early that *Dichograptus octobrachiatus* and the more profusely branching *D. logani* characteristically have a central disc composed of a double membrane. He found (2) central discs with more angular outlines on species of *Tetragraptus* such as *T. crucifer* and *T. headi*, but on *T. alatus* a relatively broad tapering membrane extends out an inch or more on each of the four branches.

In the *Phyllograptus* shales of Christiana, Norway, Herrmann discovered a large central disc on *Dichograptus kjerulfi*, a form with 12 branches, which has been refigured in a translation by Dallas (3). This species was described by Herrmann under the name of *Loganograptus kjerulfi*, under which name a specimen with the central discs highly developed and well preserved has recently been described and illustrated by Monsen (4).

Doubtless the most important information ever secured concerning synrhabdosomes was that discovered by Ruedemann (5) concerning the diprionidian graptolites *Glossograptus quadrimucronatus* and *Lassiograptus eucharis*, then known as *Diplograptus pristis* and *D. ruedemanni*. He found, in addition to the well-developed pneumatocysts, a number of beautifully preserved gonangia containing numerous young siculae attached to clublike structures, and others from which siculae had evidently just swarmed out in great numbers. The discovery of the development of siculae in large numbers in gonangia was of major biologic importance, as it associates them more closely through this apparent sexual process of reproduction with the hydrozoan group, with which they seem most closely related because of their general physiological and structural characteristics.

When the writer discovered and described the new species *Amplexograptus maxwelli* (6) from the upper part of the Bromide for-

mation in the Criner Hills of Oklahoma, he suggested, because of the radiating position of the fragmental rhabdosomes in the tough limestones, that they probably occurred in a synrhabdosome. Two years later, when the species was illustrated and described by Ekström (7) from Sweden, a synrhabdosome with 17 rhabdosomes was found in the shale. A smaller synrhabdosome preserved in pyrite has a circular elevation, 3 mm in diameter, which Ekström believed to represent a pneumatocyst.



FIGS. *1–6—Linograptus phillipsi* var. *multiramosus* Decker. ×9. Views of central portions only, to show the pneumatocysts. Henryhouse Shale (Silurian), NW corner sec. 1, T. 3 S., R. 2 E., Carter County, Oklahoma. Univ. of Oklahoma Mus. Invertebrate Paleontology, hypotypes A2473–A2478. Camera lucida drawings made by Helen Tappan with a Lapworth-Parkes graptolite microscope.

Elles and Wood (8) discovered central discs on *Dichograptus octobrachiatus* and *Trochograptus diffusus*. They also found air sacs on the individual rhabdosomes at the sicular end of *Climacograptus bicornis* var. *peltifer*, *C. wilsoni*, *C. antiquus* var. *bursifer*, and *Dimorphograptus physophora* (9). Ruedemann (10) shows a chitinous disc attached to the sicular end of several individuals of *Dictyonema flabelliforme*, *Staurograptus dichotomous*, *Bryograptus lapworthi*, *Tetragraptus fruticosus*, *T. similis*, *T. pygmaeus*, *Didymograptus patulus*, *D. extensus*, *D. nitidus*, and *Dichograptus octobrachiatus*. Tornquist (11) illustrated *Dichograptus octobrachiatus* and *Tetragraptus vestrogothus* from Sweden, with central discs.

In later horizons, Ruedemann (12) illustrates synrhabdosomes with pneumatocysts and gonotheca of *Orthograptus calcaratus* var. *incisus*, *Glossograptus quadrimucronatus* var. *approximatus*, *Lassiograptus eucharis*, a distal expansion of the nemacaulus of *Climacograptus parvus*, and proximal expansions of the proximal sicular end of *Climacograptus bicornis*, and especially in the variety *peltifer*. He has also illustrated a beautifully symmetrical synrhabdosome (13) of *Climacograptus parvus* with a central disc and about 40 radiating rhabdosomes, both old and young, of various lengths. This indicates that the individual rhabdosomes developed successively instead of simultaneously.

Doubtless most of these membranous expansions were sufficiently buoyant to float the graptolites at or near the surface of the ocean, thus enabling them to be distributed readily by winds and currents. The fact that relatively few synrhabdosomes have been found with pneumatocysts attached may possibly be explained by the delicacy of the air sacs, which may have disintegrated readily after the compound colonies matured, or they may have been easily destroyed by storm waves on the ocean.

The forms illustrated in figures 1 to 6, represent a few of the colonies of *Linograptus phillipsi* var. *multiramosus* (14), which were collected on the south side of Cool Creek, Carter County, Oklahoma, near the southern edge of the Arbuckle Mountains, where they occur in dark-gray calcareous shale about 8 feet above the base of the Silurian Henryhouse shale. Practically every compound colony of this variety exhibits a central ring or disc from which the individual stipes radiate. The three specimens shown in figures 1, 3 and 6 have radiating

ribs, which may have been supports for the top of the disc, or which may represent remnants of gonotheca. The ringlike structures shown in figures 2 and 4 may represent the edges of gonothecal sacs. On the specimens shown in the first four figures, much of the membrane of the pneumatocysts is preserved, but on the others only small parts of it remain. These compound colonies are fairly common in the one foot of shale containing them. Sometimes two or three are found on a slab 3 or 4 inches square.

This seems to be the first discovery of a pneumatocyst on a monograptid-linograptid type, and is noteworthy because of the great number of monograptids in the Silurian, especially of Great Britain and continental Europe.

Some small discs have also been discovered on the less profusely branched *Linograptus phillipsi*, a few of which are found with the more common many-branched form. The form and branching of the last-named species is very similar to *Linograptus posthumous* from Bohemia, which was illustrated in Boucek's (15) monograph on the Cyrtograptidae.

Grateful acknowledgement is made to J. O. Beach, Henry Phillips and Brooks Pierce for assistance in the field, to Helen Tappan for making the drawings, and to C. B. Bolar for photographing the plate. Funds for part of the field expenses were provided by the Oklahoma Geological Survey, the U. S. National Research Council, the Oklahoma Academy of Science, and the University of Oklahoma Research Fund.

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DEVONIAN RUGOSE CORALS FROM THE TRAVERSE BEDS OF MICHIGAN

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ABSTRACT—A three-fold division of the Middle Devonian Traverse beds of the northwestern part of the Lower Peninsula of Michigan is suggested. The rugose corals indicate that the Traverse beds were contemporaneous with the Hamilton group of New York and the Cedar Valley formation of Iowa. Two new genera and nine new species are described and figured. In view of the chaotic state of the taxonomy of rugose corals no attempt is made to assign the genera to families (the established families are polyphyletic), but their relationships are determined as far as possible. Turbidity of the water may have been a controlling factor in determining the form of the colony. Variation in solitary species may be due to differential growth, crowding, gerontism, and reproductive precosity. *Diversophyllum traversense* may be the solitary ancestor of the Mississippian compound genus *Lithostrotion*. The author of *Heliophyllum* is Dana rather than Hall.

THE TRAVERSE BEDS, at their type locality, comprise a series of calcareous shales and limestone cropping out on the shores of Grand Traverse and Little Traverse bays in the counties of Charlevoix and Emmet at the northwestern extremity of the Lower Peninsula of Michigan. The lower limits of the Traverse are not exposed; the upper limits are defined by the Waverlian black shales. On the west the area of outcrop is limited by Grand Traverse Bay; on the east by a thick overburden of drift. There is evidence to indicate that the Traverse beds are continuous under the drift with other limestones and shales on the eastern side of the Lower Peninsula. Some workers have extended the Traverse to include beds in western Ontario. The lithologic and faunal discrepancies are so marked however, that the writer feels that the name "Traverse" should be restricted to the western side of the Lower Peninsula.

The Traverse beds have been a subject for study by geologists for nearly 100 years, during which period much material has been published. Alexander Winchell (1866), in the appendix to a report on the Traverse Bay region, described, briefly and without benefit of published illustrations, 62 new species of fossils from the Traverse. Carl Rominger (1876) published the results of a geological survey of the Lower Peninsula and included a monographic work on the fossil corals of Michigan, among which many Traverse forms were described and figured. Rominger relied almost entirely on external form for identification, and, although his figures are excellent, in many cases they fail to exhibit the diagnostic features. Many other workers have contributed shorter papers on the paleontology and stratigraphy of the Traverse. M. A. Fenton (1931) has described a stromatoporoid reef, C. F. Deiss (1932) the fenestelloid Bryozoa, G. M. Ehlers and T. E. White (1935) two rugose corals, R. W. Imlay (1935) a brachiopod, Ehlers and V. Kline (1935) revised Winchell's brachiopod types, and the ostracods have been worked by A. S. Warthin (1935).

E. R. Pohl (1929) has divided the Traverse into three stratigraphic units: the Gravel Point stage at the base, the Charlevoix stage in the middle, and the Petoskey formation at the top. The writer was unable to locate the "prominent angular unconformity" at the top of the Charlevoix stage mentioned by Pohl and believes that Pohl was confused by unusually high initial dips prevailing in the area due to the proximity of large bioherms. Until more and better evidence is brought forward the writer does not feel that the term "formation" is applicable to the beds involved; instead, it is proposed for the purposes of this paper to consider all three divisions as faunal zones.

The Gravel Point zone of the Traverse is correlated with the Alpena limestone of the eastern side of the Peninsula on the basis of the occurrence in each of the short-ranged coral *Heliophyllum juvene* (Rominger). Other diagnostic occurrences common

to the Alpena and Gravel Point are *Diversophyllum traversense* (Winchell) and *Chonophyllum ponderosum* (Rominger). Warthin and Cooper (1935) state that the upper part of the Alpena limestone may be correlated with the "coral zone" beds at Widder, Ontario, and the Centerfield member of the Ludlowville formation of the New York Hamilton. The writer has identified the Gravel Point zone species, *Heliophyllum juvene*, among corals from the "coral zone" beds at Widder associated with *Heliophyllum halli* forma *arachne*, a typical Ludlowville coral. A correlation between the Petoskey zone of the Traverse and the Potter Farm formation of the eastern side of the Peninsula is indicated by the occurrence in both of two species, *Disphyllum panicum* and *Hallia vesiculata*, n. sp. The Potter Farm formation overlies beds that have been shown to be Ludlowville in age by Warthin and Cooper (1935). Thus it would appear that on the basis of the rugose corals the Traverse beds should be considered Hamilton in age and correlative, at least in part, of the Ludlowville formation. In this connection it is interesting to note that except for the omnipresent *Cystiphyllum* not a single New York species of rugose coral is known from the Traverse beds, a few are found in eastern Michigan, and many species are common to Ontario and New York. A reason for this westward change in the fauna may be found in the influence exerted by the rising landmass of Appalachia, which flooded the Appalachian trough with clastic debris while the western portion of the seaway remained clear. Vaughan (1919) has demonstrated the extreme sensitivity of corals to turbidity.

The unpublished work of A. W. Slocom on proetid trilobites and Thomas (1920) on echinoderms has indicated that a relationship exists between the Devonian of Michigan and that of Iowa. With this in mind, the writer investigated the rugose coral fauna of certain horizons in the Iowa Devonian and found that a correlation between the Traverse beds and the Cedar Valley formation is indicated. The most diagnostic occurrence in the Cedar Valley is that of *Diversophyllum traversense* (Winchell), a species characteristic of the Gravel Point zone of the Traverse. The Iowa form differs slightly in that it lacks the thick epitheca of the typical Traverse specimens, but this feature is one that would be subject to environmental control. Gerontic specimens from the type locality lack a thick epitheca and exhibit a lonsdaleiod proximal retreat of the septa; the latter character is also found in the Cedar Valley *Diversophyllum*. Also present in the Cedar Valley are an *Aulacophyllum* resembling *A. hemicrassatum*, n. sp., of the Petoskey zone, and a species resembling *Aulacophyllum mesodilatum* n. sp. of the Gravel Point. The abundant *Prismatophyllum* of the Cedar Valley appears to be intermediate between *P. davidsoni* of the Onondaga and *P. percarinatum*, n. sp. of the Traverse. *Cystiphyllum americanum* is common to both areas. Thomas (1920, p. 409) considered the Cedar Valley to be late Devonian in age because of its position above the *Hypothyridina cuboides* zone; this determination has been followed by most later workers, including Stainbrook (1935, p. 255) who placed the Cedar Valley above the Independence shale, which he believed to be the base of the Upper Devonian in Iowa. If the apparent correlation of the Cedar Valley with the Traverse is valid, a Hamilton age for the Cedar Valley is indicated, thus casting doubt on the value of *Hypothyridina* as a marker.

CLASSIFICATION OF RUGOSE CORALS

It was the practice among the early coral workers to assign all rugose coral genera to about five families. As more corals were described, however, it became increasingly difficult to define the boundaries of the families. The British workers on Carboniferous corals soon recognized that the families were polyphylletic, and that forms of the same lineage could vary widely in appearance while species of greatly different origin could, through convergence, look very similar. Lang (1917) was among the first to recognize convergence among rugose corals, and after a study of other groups he came to the conclusion that the evolution of organisms may follow trends, independent of natural selection, and that the trends might be followed a long way before ultimate extinction befell the organism through the development of nonviable end products of the trends. Applying this doctrine Lang (1923) listed eight trends exhibited by rugose corals. The writer is not in a position

to criticize the theory from a purely biologic standpoint, but to the systematist it offers, by listing the trends a genus or species seems to follow, a means of eliminating a good deal of wordy description. The application of the theory also offers the best approach to the problem of rugose coral phylogeny. At the present time not nearly enough is known to attempt a reconstruction of Devonian coral phylogenesis, but it seems probable that after a few more years of work such as is being done in England by W. D. Lang and Stanley Smith it will be possible to divide properly the present polyphyletic genera and to assign each species to its correct stock. For the purposes of this paper the genera are not assigned to families, but they have been established along the time-accepted, probably erroneous, plan. The writer recognizes this deficiency but is unable to correct it at present.

ACKNOWLEDGMENTS

From the winter of 1935 to the spring of 1937 the writer studied Traverse corals at Walker Museum, University of Chicago, under the direction of Dr. Carey Croneis to whom the writer is pleased to acknowledge a great debt for the many hours of consultation and assistance rendered during the course of the research. The writer is greatly indebted to the late Mr. A. W. Slocom of Walker Museum for his aid in collecting material during the field season of 1936. The writer owes further thanks to Dr. G. M. Ehlers of the University of Michigan for the identification of Winchell's and Rominger's types, for the loan of photographs and permission to reproduce them here, and for two invaluable days during which the problem was discussed and many pertinent suggestions offered; to Dr. G. Arthur Cooper for the loan of specimens from the U. S. National Museum and for very valuable help rendered during two days in the field; to Dr. W. C. Allee of the Department of Zoology of the University of Chicago for information pertaining to ecology, variation and speciation; and to Drs. W. D. Lang and H. Deighton Thomas for very helpful criticism of the subject during two days spent at the British Museum (Natural History).

Topotype material and nitrocellulose peels taken from the type specimens of the species described in this paper are to be deposited at the following institutions: Walker Museum, University of Chicago; University of Michigan, Ann Arbor; Stanford University, California; United States National Museum, Washington, D. C.; British Museum (Natural History), London.

SYSTEMATIC DESCRIPTIONS

Genus TORTOPHYLLUM Sloss, n. gen.

Genotype, *Tortophyllum cysticum* (Winchell).

Solitary corals with numerous steeply inclined rows of globose dissepiments, tabulae differentiated into a horizontal periaxial series and an inclined axial series, which is reflected in the calyx by a low calicular boss. The major septa extend to the axis, where they are twisted and joined together into a loosely knit axial complex. Minor septa characteristically long; dissepimentarium correspondingly wide. The corallum is without apparent symmetry and lacks a cardinal fossula, thus differing from *Phaulactis* Ryder (1926, p. 385).

Discussion.—The genus is evidently the result of aulophylloid and cystiphylloid trends. The first is evident in the structure of the axial complex, the second in the large number of dissepiments and the characteristically incomplete tabulae. Morphologically the genus is intermediate between a simple cyathophylloid and a complex clisiophylloid, but whether or not this represents the true phylogenetic position will not be known until more species are recognized and the trends established.

Superficially the genus resembles a large noncarinate *Macgeea*. Both forms have long, tapering septa, numerous concentric, globose dissepiments. Certain genera related to *Macgeea* lack horseshoe dissepiments and have differentiated tabulae as in *Tortophyllum*. The prominent trabeculae of the latter may represent incipient or vestigial carinae.

Occurrence.—The genus is known at present only from the Gravel Point and Petoskey zones of the Traverse in the Petoskey area, and from the Alpena limestone of the eastern area.

TORTOPHYLLUM CYSTICUM (Winchell)

Plate 11, figures 1–12, text figure 1

Zaphrentis cystica WINCHELL, *1866*, The Grand Traverse Region, p. 90.

Lectotype.—Alma College, Michigan. One of two specimens in the Alma College collection marked 2724-t (for type). The lectotype is a small specimen cut longitudinally and transversely to show a section through the calyx and half of a transverse section. The specific characters are readily apparent. The other specimen is not sectioned but is obviously *Diversophyllum traversense* (Winchell). No locality number is given.

Original description.—Outer zone of finely vesicular tissue reaching nearly halfway to the center; central septa very thin and irregular; lamellae about 60, of which half terminate with the vesicular zone.

This inadequate description is not accompanied by any figures, published or unpublished. Therefore, it is necessary to append the following revised description.

External characters: Corallum simple, curved ceratoid to straight cylindrical. Maximum observed size 170 mm high, 60 mm in diameter; average 100 mm by 40 mm. Specimens commonly decorticated; where present, epitheca exhibits fine septal grooves, broad interseptal ridges, annular growth lines, and deep constrictions of rejuvenescence. Calyx depth equal to radius of corallum, walls descend abruptly from periphery to concave calicular pit; center occupied by low, rounded, calicular boss. Major septa straight, unornamented peripherally; join, twist, and become involved with other structures at axis. If twisting of distal ends of majors is prominent tortion is always counterclockwise. Minor septa much less prominent than majors.

Transverse section: Thirty-eight to 46 major septa present; number varies with size and age of individual. Neanic stage of rare individuals exhibits cardinal, counter and alar septa; ephebic sections of all specimens retain no semblance of symmetry. Major septa extend to axis, where they characteristically join, twist, and become involved with elements of the tabularium to form ill-defined axial complex. Septa slightly dilate in dissepimentarium, taper rapidly in tabularium. Occasionally within dissepimentarium, more commonly at inner limit of dissepimentarium, septa are involved with one ring of dissepiments in a narrow stereozone. Average length of minor septa equal to one-third radius, may extend to over two-thirds radius or be restricted to narrow peripheral border. Dissepiments numerous, concentrically arranged. Truncated edges of tabulae appear as concentric structures in tabularium.

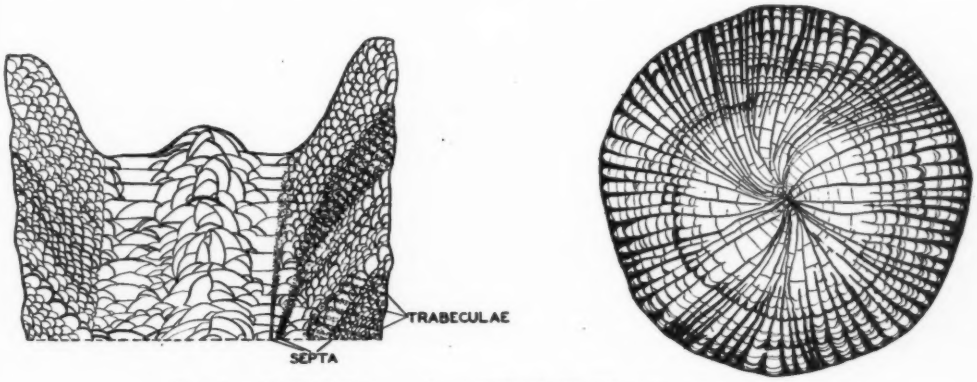

FIG. 1.—*Tortophyllum cysticum* (Winchell). Diagrammatic longitudinal and transverse sections, enlarged.

Longitudinal section: Dissepiments numerous, small, globose, arranged in steeply inclined rows. Width of dissepimentarium varies with length of minor septa; may occupy wide border on either side of section or be restricted to three-millimeter-wide band. Tabulae characteristically incomplete, poorly differentiated into subhorizontal periaxial series and steeply inclined or domed axial series. Differentiation much more prominent in specimens with wide dissepimentaria.

When plane of section intersects plane of septum lying essentially parallel to it, septum exhibits prominent trabeculae spaced

0.5 mm apart, arched like carinae of *Heliophyllum*.

Discussion.—The species exhibits a wide range of variation in form and internal structure. If only a small collection were available, it would be a simple matter to define several species, but the study of a large number of specimens indicates that all the variants intergrade.

The species is very common in the upper half of the Gravel Point zone of the Traverse and is particularly characteristic of the "upper blue shale" at the top of the zone. Rare specimens are known in a large collection from the Petoskey zone; these all exhibit extreme break-down of the tabulae into tabellae and extreme doming in the axial area. Both these characters are considered by the writer to represent an advance over the more complete tabulae and less domed condition of the Gravel Point forms. It is possible that the Petoskey forms

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EXPLANATION OF PLATE 9

FIGS. *1–8—Streptelasma petoskeyense* Sloss, n. sp. Petoskey zone, U. S. Highway 31, 200 yards east of intersection of Michigan Highway 131, NE ¼ of NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich. *1, 2*, Paratype (U. C. 38714), peels of longitudinal and transverse sections, ×1; *3*, holotype (U. C. 38715), peel of longitudinal section, ×1; *4*, paratype (U. C. 38716), thin section of immature transverse section, ×1; *5*, paratype (U. C. 38717), peel of longitudinal section, ×1; *6*, paratype (U. C. 38718), peel of longitudinal section, ×1; *7*, paratype (U. C. 38719), view of calyx, ×½; *8*, paratype (U. C. 38720), lateral view, ×½. (p. 61)

9, 10—Aulacophyllum hemicrassatum Sloss, n. sp. Gravel Point zone, west end Petoskey Portland Cement Company quarry, SW ¼ sec. 2, T. 34 N., R. 6 W., Emmet County, Mich. Holotype (U. C. 38709), peels of longitudinal and transverse sections, ×1. (p. 64)

11–13—Aulacophyllum mesodilatum Sloss, n. sp. Gravel Point zone, Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich. *11, 12*, Holotype (U. C. 38704), calicular and lateral views, ×½; peel of transverse section of holotype, ×1. (p. 65)

14–17—Heliophyllum juvene (Rominger). Gravel Point zone, Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich. *14*, Hypotype (U. C. 38706), peel of longitudinal section, ×1; *15*, hypotype, (U. C. 38707), peel of transverse section, ×1; *16*, hypotype (U. C. 38705), thin section of longitudinal section, ×1; *17*, calicular view of same specimen as *15*, ×½. (p. 58)

18–20—Aulacophyllum bilaterale Sloss, n. sp. Petoskey zone, U. S. Highway 31, 200 yards east of intersection of Michigan Highway 131, NE ¼ of NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich. Holotype (U. C. 38710), peels of longitudinal and transverse sections, ×1. (p. 64)

21, 22—Chonophyllum ponderosum Rominger. Gravel Point zone, Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich. Hypotype (U. C. 38700), calicular and lateral views, ×½. (p. 59)

23, 24—Chonophyllum ovatum Sloss, n. sp. Gravel Point zone, Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich. Holotype (U. C. 38702), lateral and calicular views, ×½. (p. 60)

25—Disphyllum panicum (Winchell). Petoskey zone, Mud Lake quarry, NE ¼ of NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich. Hypotype (U. C. 38711), thin section, ×1. (p. 68)

26, 27—Disphyllum panicum (Winchell). Petoskey zone, Northern Lime Company quarry, Petoskey, NE ¼ sec. 32, T. 35 N., R. 5 W., Emmet County, Mich. Hypotype (U. C. 38712), transverse and longitudinal sections, ×1.

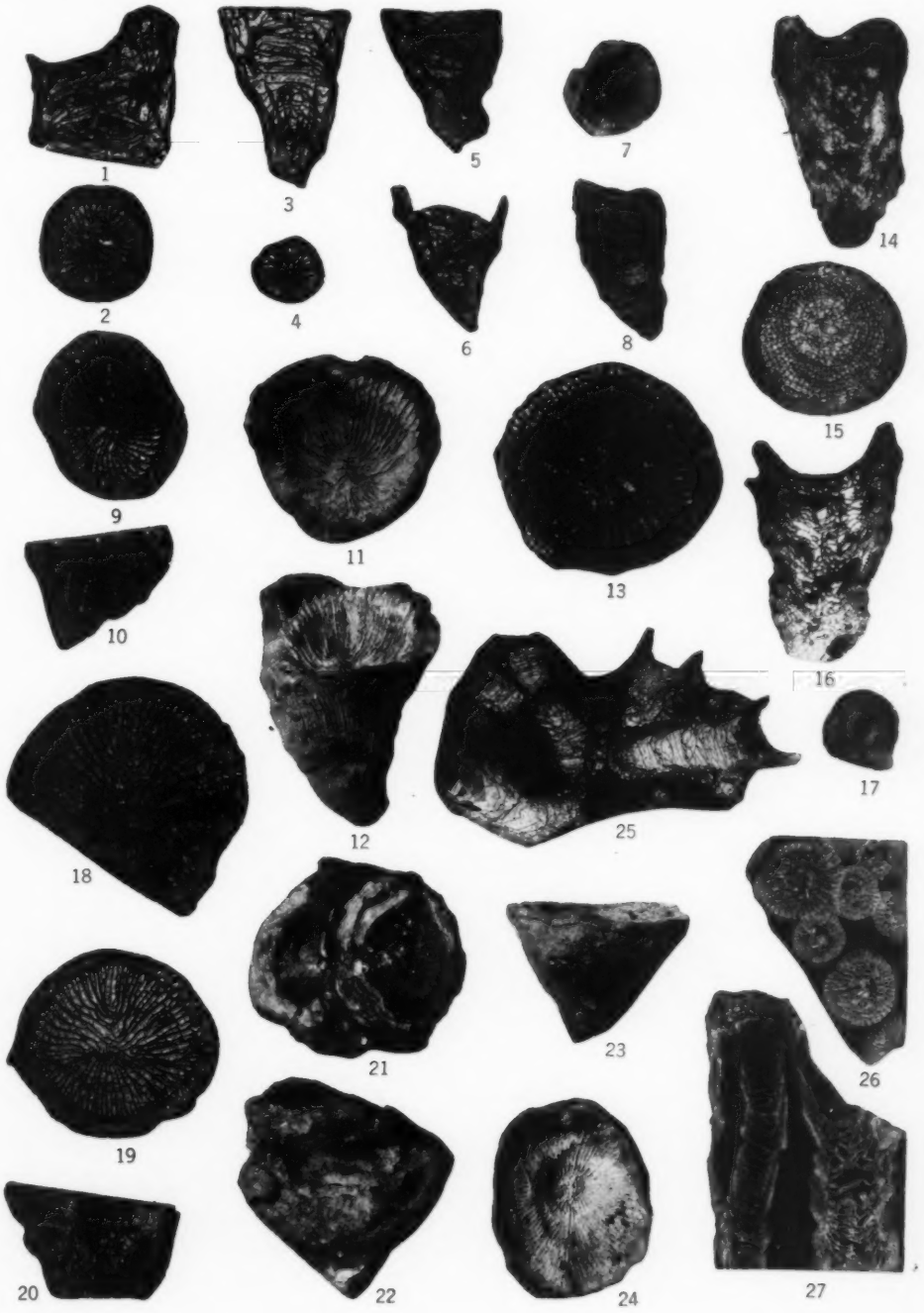
EXPLANATION OF PLATE 10

FIGS. *1–5—Prismatophyllum cristatum* (Rominger). Gravel Point zone, Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich. *1*, Hypotype (U. C. 38745), ×½; *2, 3*, same specimen, peels of longitudinal and transverse sections, ×1; *4, 5*, hypotype (University of Michigan), thin sections of transverse and longitudinal sections (photographs courtesy G. M. Ehlers), ×1. (p. 71)

6–9—Prismatophyllum percarinatum Sloss, n. sp. Gravel Point zone, Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich. *6*, Holotype (U. C. 38746), ×1; *7*, paratype (U. C. 38747), thin section, ×1; *8*, paratype (U. C. 38748), thin section, ×1; *9*, paratype (U. C. 38749), thin section ×1. (p. 69)

10–13—Prismatophyllum pauciseptatum Sloss, n. sp. Petoskey zone, Mud Lake quarry, NE ¼ of NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich. *10–12*, Holotype (U. C. 38752), peels, ×1; *13*, holotype, ×½. (p. 70)

14—Prismatophyllum cristatum microcarinatum Sloss, n. var. Gravel Point zone, Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich. Holotype (U. C. 18402), ×½. (p. 72)



Sloss, Devonian Corals

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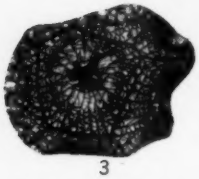
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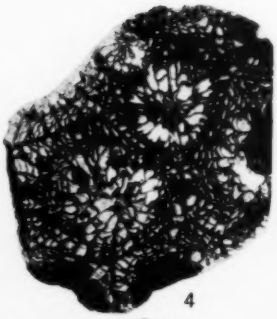
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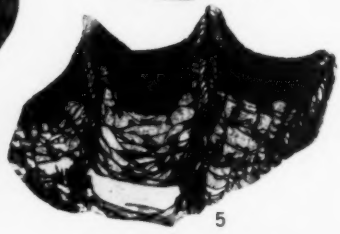
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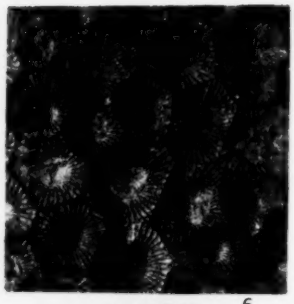
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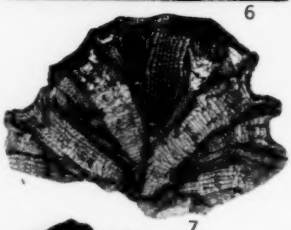
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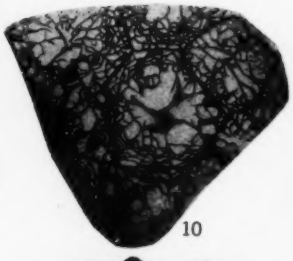
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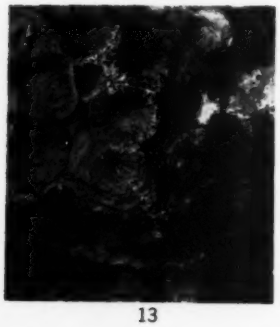
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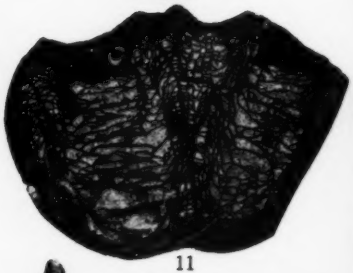
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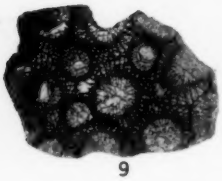
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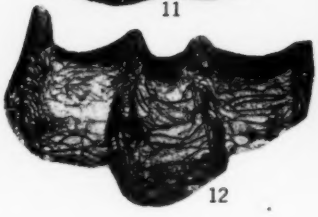
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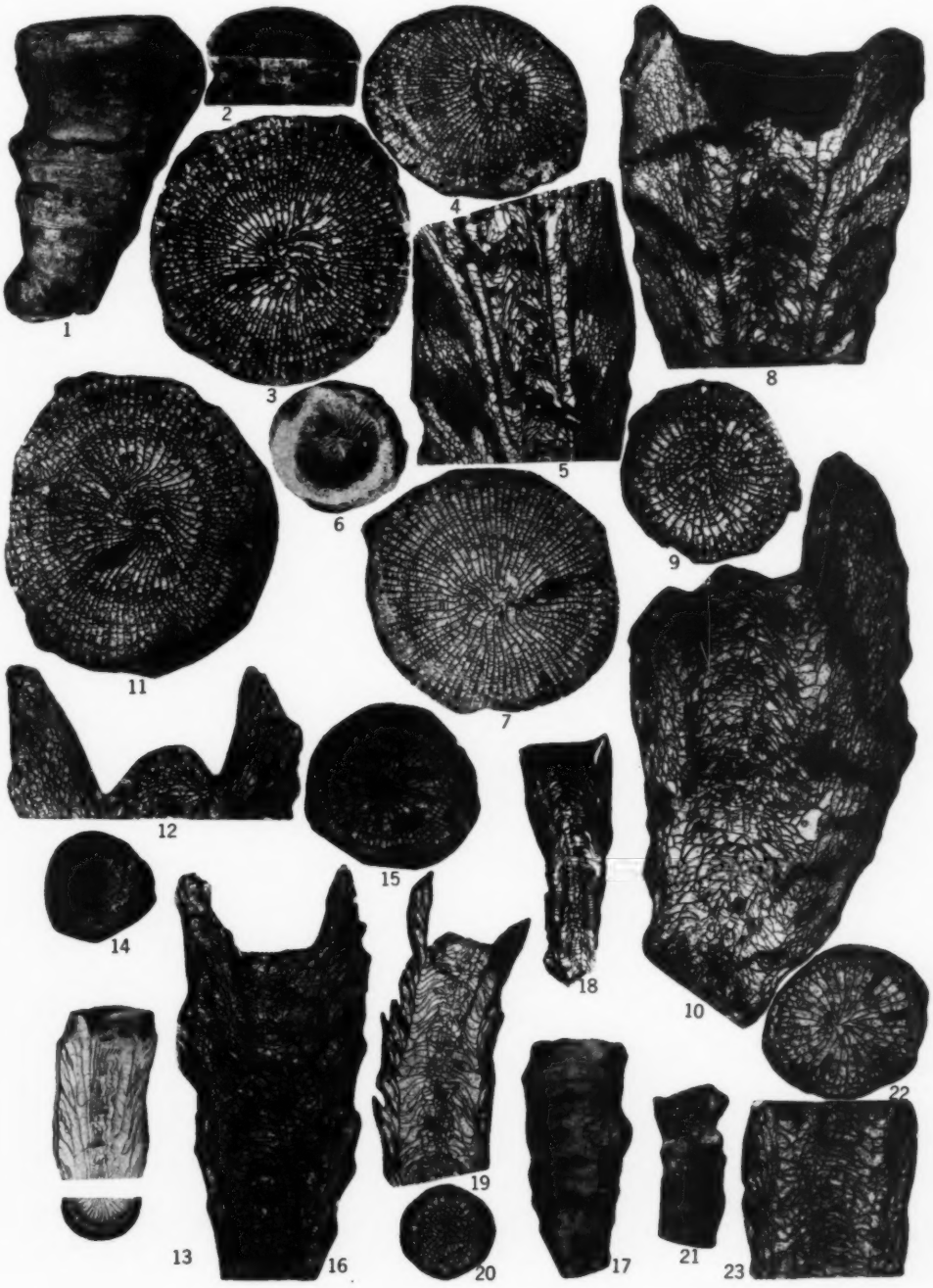
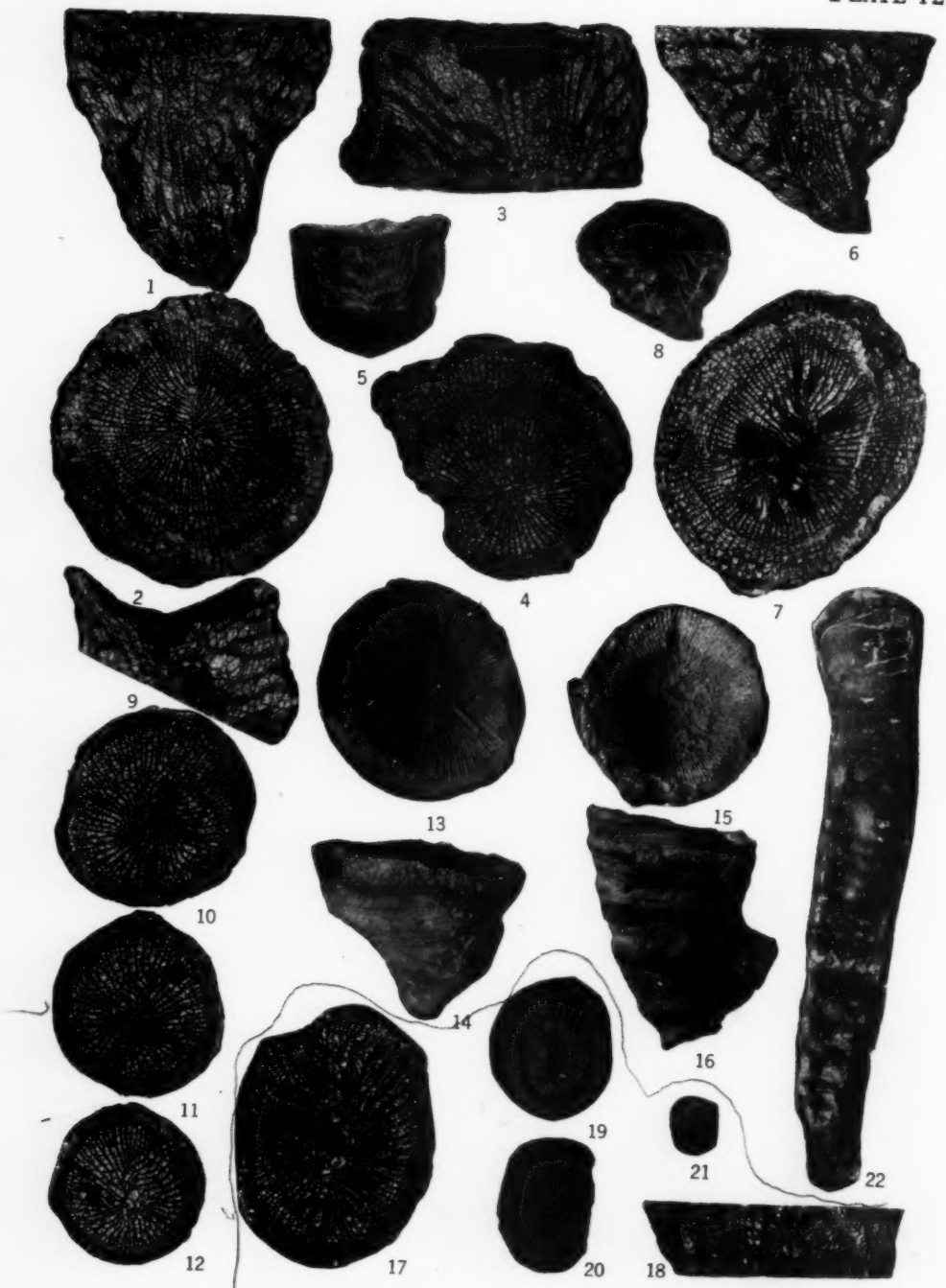
Sloss, Devonian Corals



Sloss, Devonian Corals



Sloss, Devonian Corals

should be separated as a distinct species.

In the lower Bell shale at Calcite, Mich., occurs a species that differs from *T. cysticum* in lacking a calicular boss and in having undomed axial tabulae.

Locality.—Winchell gives no locality for the single specimen in his collection, so the type locality for the species must remain unknown. It is probable, however, that the lectotype was collected from the lake-cliff outcrops of the Gravel Point at Petoskey, Mich.

Specimens in the writer's collection are from the following localities:

Gravel Point Zone

Bell quarry, 2.3 miles east of Charlevoix county line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich.

Lake cliffs at Bay View Station of Pennsylvania Railroad. NW ¼ sec. 32, T. 35 N., R. 5 W., Emmet County, Mich.

West end Petoskey Portland Cement Company quarry. SW ¼ sec. 2, T. 34 N., R. 6 W., Emmet County, Mich.

Petoskey Zone

"Mud Lake" quarry. East Bay View (Kegomic), Mich. NE ¼ of NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich.

Repository of type material.—Lectotype;

EXPLANATION OF PLATE 11

FIGS. *1–10—Tortophyllum cysticum* (Winchell). Gravel Point zone, I. Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich. *1*, Hypotype (U. C. 38624), ×½; *2*, section of same specimen, ×½; *3*, peel of transverse section of same specimen, ×1; *4*, peel of transverse section of hypotype (U. C. 38725), ×1; *5*, thin section of longitudinal section, same specimen, ×1; *6*, hypotype (U. C. 38726), view of eroded calyx, ×½; *7*, hypotype (U. C. 38727), peel of transverse section, ×1; *8*, hypotype (U. C. 38728), peel of longitudinal section, ×1; *9*, same specimen, thin-section of immature transverse section, ×1; *10*, hypotype (U. C. 38729), peel of longitudinal section, ×1. (p. 54)

11, 12—Tortophyllum cf. *T. cysticum* (Winchell). Petoskey zone, Mud Lake quarry, NE ¼ of NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich. Peels of longitudinal and transverse sections of a specimen (U. C. 38732), doubtfully referred to the species, ×1. (p. 54)

13—Diversophyllum traversense (Winchell). Previously unpublished drawing made for Winchell at time of original description of the holotype of the species but not included in original publication; bears Winchell's handwritting, designating the type specimen, which is now at the Hood Museum, Alma College, Mich. Drawing at University of Michigan. (Photograph courtesy G. M. Ehlers.) (p. 66)

14–23—Diversophyllum traversense (Winchell). Gravel Point zone, Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich. *14*, Hypotype (U. C. 38733), view of the calyx, ×½; *15*, same specimen, peel of transverse section, ×1; *16*, hypotype (U. C. 38734), peel of transverse section of specimen with flat tabulae and wide dissepimentarium, ×1; *17*, lateral view of the same specimen, ×½; *18*, hypotype (U. C. 38735), thin-section of longitudinal section of specimen exhibiting highly domed tabulae and a restricted dissepimentarium, ×1; *19, 20*, hypotype (U. C. 38736), peels of longitudinal and transverse sections, ×1; *21*, side view of same specimen showing lateral bud, ×½; *22, 23*, hypotype (U. C. 38737), peels of transverse and longitudinal sections of a specimen exhibiting intermediate characters, ×1. (p. 66)

EXPLANATION OF PLATE 12

FIGS. *1–8—Hallia vesiculata* Sloss, n. sp. Petoskey zone, NE ¼ of NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich. *1, 2*, Holotype (U. C. 38738), peels of transverse and longitudinal sections, ×1; *3, 4*, paratype (U. C. 38739), peels of longitudinal and transverse sections, ×1; *5*, same specimen, ×½; *6, 7*, paratype (U. C. 38753), peels of longitudinal and transverse sections, ×1; *8*, same specimen, ×½. (p. 62)

9–12—Hallia vesiculata Sloss, n. sp. Petoskey zone, U. S. Highway 31, 200 yards east of intersection of Michigan Highway 131, NE ¼ of NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich. Paratype (U. C. 38742), peels of longitudinal and transverse sections of an immature specimen, ×1. (p. 62)

13–16—Hallia vesiculata Sloss, n. sp. Petoskey zone, Mud Lake quarry, NE ¼ of NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich. *13, 14*, Paratype (U. C. 38740), ×½; *15, 16*, paratype (U. C. 38741), ×½. (p. 62)

17–21—Hallia zonata, Sloss, n. sp. Petoskey zone, Mud Lake quarry, NE ¼ of NW ¼ sec. 34. T. 35 N., R. 5 W., Emmet County, Mich. *17, 18*, Holotype (U. C. 38743), peels of transverse and longitudinal sections, ×1; *19–21*, holotype, ×½. (p. 63)

22—Diversophyllum traversense (Winchell). Gravel Point zone, west end Petoskey Portland Cement Company quarry, SW ¼ sec. 2, T. 34 N., R. 6 W., Emmet County, Mich. Hypotype, (U. C. 38744), ×½. (p. 66)

Alma College, Alma, Mich. Hypotypes, Walker Museum, Univ. of Chicago.

Genus HELIOPHYLLUM Dana, 1846

DANA, *1846*, U. S. Exp. Ex. VIII, "Zoophytes," p. 356, pl. 26, fig. 3. Emend. MILNÉ-EDWARDS and HAIME, *1850*, British Fossil Corals, pp. lxix, 235.

Genotype, *Heliophyllum halli* Milne-Edwards and Haime, 1850.

Original description.—From the discussion of the genus *Cyathophyllum* in Dana's "Zoophytes" (1846, p. 356):

> There are others in which the dissepiments run *upward* and inward, as represented in plate 26, figures 3, 4, and 4a; and as the species have also some difference in habit, they constitute a subgenus, if not a wholly distinct group. The name *Heliophyllum* has been applied by Mr. James Hall to a specimen of this kind in his cabinet, and may well be retained. It is represented in his N. Y. Geological Report, fig. 3, p. 209, and is probably near the *Cyathophyllum helianthoides* of Goldfuss, plate 20, fig. 2.
>
> The subgenus *Heliophyllum* will then contain species having generally the transverse septa of the Cyathophylla, but with the intermediate dissepiments running oblique *upward* and inward.

Emended description.—Corallum simple. Septal apparatus well developed, and producing lateral lamellar prolongations, which extend from the wall towards the centre of the visceral chamber, so as to represent ascending arches, and to constitute irregular central *tabulae*, and which are united towards the circumference by means of vertical dissepiments (Milne-Edwards and Haime, 1850, p. lxix).

Discussion.—Previous workers have been unanimous in considering *Heliophyllum* as one of Hall's genera, but in the opinion of the writer this is erroneous. Hall is responsible for the name but used it only on a museum specimen and in conversation with Dana; he was not responsible for the generic diagnosis or figure published by Dana.

On this point the International Rules of Zoological Nomenclature read as follows:

> Article 21.—The author of a scientific name is that person who first publishes the name in connection with an indication, a definition, or a description, unless it is clear from the contents of the publication that some other person is responsible for said name and its indication, definition, or description.

The meaning of the word "indication" with regard to generic names is construed by the International Commission on Zoological Nomenclature as follows:

> (1) A bibliographic reference, or (2) a definite citation of an earlier name for which a new name is proposed, or (3) the citation or designation of a type species.
>
> In no case is the word "*indication*" to be construed as including museum labels, museum specimens, or vernacular names.

By monotypy the species described and figured by Hall (1843, p. 209) as *Strombodes helianthoides* (Goldfuss) is the genotype. Hall identified the New York form in question from a description and figure published by Phillips (1841, p. 10), who identified his specimens as *Cyathophyllum helianthoides* Goldfuss, but referred the species to the genus *Strombodes* Schweigger. Milne-Edwards and Haime (1850) upon examining Phillips' specimens discovered that they were misidentified, thus making *Heliophyllum helianthoides* a homonym. This they rectified by renaming the species *H. halli.*

Heliophyllum is represented by one species in the Traverse. Many species have been described from the Hamilton group, but Wells (1937) has shown that, at least for a single horizon, only one biologic unit is present and the other "species" are of varietal rank.

HELIOPHYLLUM JUVENE (Rominger)
Plate 9, figures 14–17

Cyathophyllum juvenis ROMINGER, *1873*, Michigan Geol. Survey, vol. 3, pt. 2, p. 101.—*Not Cyathophyllum juvene* DAVIS, *1885*, Kentucky Fossil Corals, pls. 79, 80.

Heliophyllum juvene CALVIN, *1888*, Am. Geologist., vol. 1, p. 83. *Fide* Whiteaves, 1898.—WHITEAVES, *1898*, Contr. Canadian Paleontology, vol. 1, pt. 5, p. 365.—*Not* WERNER, *1932*, Washington Univ. [St. Louis] Studies, new ser., no. 7, p. 117.

Syntypes.—Rominger's types are at the University of Michigan. No type locality is given, the type specimens being collected from Widder, Ontario, and Little Traverse Bay.

External characters: Corallum simple, curved ceratoid. Average height 50 mm, diameter 20 mm. Epitheca thin, with faint septal grooves and growth lines. Coarse rugae indicate periodic rejuvenescence of corallum. Calyx depth about equal to radius; walls descend in convex curve to small concave calicular floor. Axis commonly eccentric in direction of curvature. Major septa approximately 30 in number, straight, persistent to axis; minors finer, shorter; both series bear denticulate edges and yardarm carinae.

Transverse section: Distal ends of major septa commonly anastomose and twine at axis. Minors extend two-thirds distance from periphery to axis. Carinae appear as opposed diamond-shaped areas on septa. Inner limit of dissepimentarium marked by ring of prominent dissepiments, other dissepiments fine, subordinate to carinae.

Longitudinal section: Carinae appear as continuous ridges on septa ascending in an arc from periphery to axis, spaced about 0.4 mm apart. Dissepiments numerous, globose, arranged in steeply dipping rows. Tabularium filled with undifferentiated tabellae.

Discussion.—The writer has compared specimens of *Heliophyllum juvene* from the Gravel Point zone (to which the species is confined in the western area) with specimens from the "coral zone" of the Widder Beds near Thedford, Ontario, and found them to be conspecific. The specimens from the upper Helderberg and Onondagan that have been referred to *H. juvene* have proved to be misidentifications in each case investigated by the writer.

H. juvene is possibly synonymous with *Heliophyllum tenuiseptatum* Billings (1859, p. 126), also described from the Hamilton of Ontario, but until Billings' type is actually compared with *H. juvene* it is safer to retain Rominger's name.

A coral that closely resembles *H. juvene* occurs in the Upper Bell formation at Rockport, Mich. The Bell species differs in having shorter septa, less prominent carinae, and more nearly complete tabulae; it may be regarded as being more primitive than *H. juvene.*

Localities.—The species is very common in the upper part of the Gravel Point zone, particularly the "blue shale" at the following localities:

Bell quarry, two miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8 T. 34 N., R. 6 W., Emmet County, Mich.

Lake cliffs at Bay View Station, Pennsylvania Railroad. NW ¼ sec. 32, T. 35 N., R. 5 W., Emmet County, Mich.

West End Petoskey Portland Cement Company quarry. SW ¼ sec. 2, T. 34 N., R. 6 W., Emmet County, Mich.

Genus CYSTIPHYLLUM Lonsdale, 1839

LONSDALE in MURCHISON, *1839*, Silurian System pt. 2, p. 691.

Discussion.—The corals that have been included in *Cystiphyllum* are the end products of cystiphylloid trends in widely separated stocks. Since most of the diagnostic characters are obliterated by the great development of undifferentiated dissepiments and tabellae the convergence of forms of varied phylogenesis is extreme. Therefore the genus can not be considered as a group of biologically related units nor can much stratigraphic significance be derived from its occurrence.

The following "species" have been recognized in the Gravel Point zone:

Cystiphyllum americanum Milne-Edwards and Haime, *1851*, Polypiers fossiles terrain paleozoique, p. 464, pl. 13.

Cystiphyllum varians Hall, *1896*, Illinois Devonian fossils, pl. 29.

Cystiphyllum cf. *C. lamellosum* (Goldfuss), *1826*, Petref. Germ., pt. 1, p. 58, pl. 18, fig. 3.

C. americanum is one of the most common fossils in the upper part of the zone.

The following species of *Cystiphyllum* occur in the Petoskey zone:

Cystiphyllum americanum

Cystiphyllum cf. *C. aggregatum* Billings, *1859*, Canadian Journ., n. ser., vol. 4, p. 137, fig. 28.

The latter form, a compound species, occurs in large masses near the base of the Petoskey zone.

Genus CHONOPHYLLUM Milne-Edwards and Haime, 1850

MILNE-EDWARDS and HAIME, *1850*, British Fossil Corals, p. 49.

Genotype, *C. perfoliatum* Milne-Edwards and Haime = *Cyathophyllum plicatum* Goldfuss, *1826*, Petref. Germ., pl. 18, fig. 5, not pl. 15, fig. 12.

Original description.—Corallum simple, and constituted principally by a series of infundibuliform *tabulae*, superposed and invaginated, the surface of which presents numerous septal radii equally developed, and extending from the centre to the circumference. No *columella* nor *walls* (Milne-Edwards and Haime, 1850, p. lxix).

CHONOPHYLLUM PONDEROSUM Rominger

Plate 9, figures 21, 22

Chonophyllum ponderosum ROMINGER, *1876*, Michigan Geol. Survey, vol. 3, pt. 2, p. 117.

Original description.—Patellate, depressed, conical polyparia of irregular, unsymmetrical, clumsy growth, with gemmation from the centre of the calyces, of new single cells, or, in rare instances, of from two to four confluent or imperfectly defined calyces. End cells shallow, explanate at the margins, more abruptly depressed

in the centre, which is surrounded by a circle of low, linear crests uniting in it with twisted ends. Expanded marginal part radiated by flat, band-like plications of papillose surface. The specimens are all formed of a heavy, compact mass of amorphous, white, ivory-like carbonate of lime, or partly silicified, and with scarcely a trace of the organic structure preserved; only in a few specimens could enough of it be seen by which to recognize the generic relations of the specimens and their correspondence with *Chonophyllum*. It does not seem to be the mode of petrifaction which obscures the structure as we find this coral in different localities associated with other corals exhibiting the finest details of structure, while they everywhere present the same massive, compact condition. The coral appears to have, during the progress of its growth, filled out its cellulose cavities as soon as the fleshy parts of the animal abandoned them.

. . . [the species] is abundant in certain layers of the Hamilton Group at Thunder Bay, and is also found at Little Traverse Bay (Rominger, 1876, p. 117).

Discussion.—The species occurs in the upper part of the Gravel Point zone, but good specimens are very scarce. The writer has hesitantly referred to this species certain incomplete coralla which appear to be young examples. These do not exhibit the repeated extreme rejuvenescence of the typical specimens, nor are they so heavily invested with structureless calcite. A coral closely resembling the Gravel Point species occurs in the upper Alpena limestone at Alpena, Michigan.

Locality.—Specimens in the writer's collection are from the "blue shale" of the Gravel Point zone at locality 1, NE$\frac{1}{4}$ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich.

Holotype.—University of Michigan, Ann Arbor. Comparative material at Walker Museum, University of Chicago.

CHONOPHYLLUM OVATUM Sloss, n. sp.
Plate 9, figures 23, 24

External characters: Corallum simple, erectly turbinate. Height of holotype 37 mm, width at cardinal septum 52 mm, at alar septa 45 mm. Epitheca smooth. Calyx shallow, calicular pit 12 mm in diameter, surrounded by broad, gently sloping calicular platform. Axis eccentric in direction of counter septum. Eighty-four septa appear as broad ridges separated by narrow grooves on calicular platform, majors project as fine blades into calicular pit, complexly intertwined at axis; minors project only slightly beyond calicular platform. Septa of cardinal quadrants pinnately arranged about long prominent cardinal septum.

Transverse section: restricted axial complex filled with intertwined distal ends of major septa. Remainder of lumen occupied by dense white organic calcite, in which interseptal loculi appear as fine dark lines.

Longitudinal section: Axial complex tapers but slightly toward base of corallum. Remainder of lumen occupied by dense, white organic calcite in which tabulae appear as closely spaced, axially inclined, fine lines.

Discussion.—The inclusion of this species in *Chonophyllum* is purely provisional. Although the *Hallia*-like character of the septal symmetry seems to indicate a generic distinction, the writer hesitates to erect a new genus on the scanty material now available. It seems probable, however, that the dense filling of the lumen represents an end stage in a petraeoid trend which might arise in several stocks.

The species is at present represented by only three specimens, all collected from the top of the Gravel Point zone.

Type locality.—Bell quarry, 2.3 mi. east of Charlevoix County line on U. S. Highway 31. NE $\frac{1}{4}$ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich.

Other locality "Upper blue shale," Gravel Point zone, lake bluffs at Bay View Station, Pennsylvania Railroad, NW $\frac{1}{4}$ sec. 32, T. 35 N., R. 5 W., Emmet County, Mich.

Type material.—Holotype and paratypes at Walker Museum, University of Chicago. Holotype, U. C. no. 38702.

Genus STREPTELASMA Hall, 1847

HALL, *1847*, Paleontology of New York, vol. 1, p. 17.

Genotype, *Streptelasma corniculum* Hall, by subsequent designation (Roemer, 1861, p. 19).

Hall's inadequate original description has been revised by Stanley Smith as follows:

Simple, trochoid or conical rugose corals, in which the more or less denticulate axial edges of the major septa twist to form a loosely built axial structure. In the brephic stages the septa are usually much dilated, and are laterally contiguous; but in the ephebic stage the dilation is generally restricted to the peripheral border,

where the short minor septa are fused to the major by stereome to form a narrow stereozone. The irregular tabulae slope downwards and towards the periphery. Dissepiments are typically suppressed (Smith, 1930, p. 311).

Discussion.—*Streptelasma* has become a waste-basket genus in which have been placed many species of structure so generalized that their true relationships are not clear. The writer realizes the probability that the genus is highly polyphylletic but is at a loss at present for a better means of disposing of a species whose structure corresponds to *Streptelasma* but whose phylogenesis is unknown.

STREPTELASMA PETOSKEYENSE Sloss, n. sp.

Plate 9, figures 1–8, text figure 2

External Characters: Corallum simple, trochoid to ceratoid; average 35 mm high, 20 mm in diameter at top of calyx. Epitheca thick, ornamented with low interseptal ridges and conspicuous growth lines. Calyx normally shallow, flat-floored, but quite variable.

Transverse section: Peripheral stereozone prominent. The 32 major septa continuous to axis in neanic and early ephebic stages, characterized by amplexoid shortening in later stages. Septa markedly dilate in early stages, relatively thin in later stages. Rare specimens exhibit poorly developed cardinal fossula occupied by a reduced septum. Minor septa visible only as fine lines in peripheral stereozone of neanic stage, extend one-third distance to axis in ephebic stabe of large specimens. Dissepiments rare.

Longitudinal section: Tabulae numerous, characteristically complete, horizontal or slightly domed. Dissepiments, if present, confined to a single subvertical row in ephebic portion of corallum.

Discussion.—The affinities of the species are unknown at present. It is hoped that future detailed work on the ontogeny of *Streptelasma* will reveal the relationships of the forms included in the group.

Type locality.—Grass-roots at roadside, and bed of small stream 1½ miles east of Bay View, on U. S. Highway 31, 200 yards east of the intersection of Michigan Highway 131. NE ¼ of NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich.

Other locality.—"Mud Lake quarry," East Bay View, NE ¼ of NW ¼ sec. 34. T. 35 N., R. 5 W., Emmet County, Mich.

Type material.—Holotype, Walker Museum, University of Chicago. U. C. no.

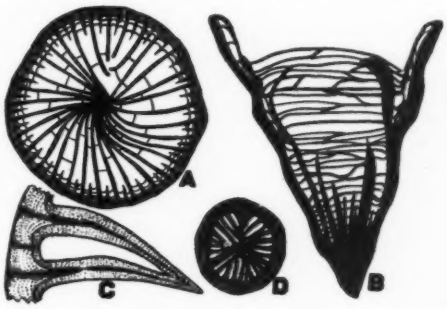


FIG. 2.—*Streptelasma petoskeyense* Sloss, n. sp. *A*, *B*, Diagrammatic transverse and longitudinal sections, ×1½; *C*, diagrammatic section through neanic septa exhibiting marked dilation, ×5½; *D*, diagrammatic neanic transverse section, ×1½.

38715. Paratypes, Walker Museum, University of Chicago.

Genus HALLIA Milne-Edwards and Haime, 1850

MILNE-EDWARDS and HAIME, *1850*, British Fossil Corals, p. lxvii.

Genotype, *Hallia insignis* Milne-Edwards and Haime.

Original description.—Corallum tall, turbinate, septa highly developed and extending to the centre of the tabulae. No columella. One remarkable large primary septum occupying the place of the septal fossula, and the neighbouring septa directed towards it so as to assume a pinnate arrangement; the septa belonging to the two other systems presenting the usual radiate position (Milne-Edwards and Haime, 1850, p. lxvii).

Discussion.—The species placed in *Hallia* by Milne-Edwards and Haime (1851, p. 353) and Hall (1882, p. 411) do not all exhibit the very prominent cardinal septum in the calyx mentioned in the original description, but all have in common a narrow groovelike fossula occupied by a long cardinal septum. This is also a character of the Traverse species, which exhibit, in transverse section, a strong cardinal septum persistent to the axis, and about which the septa of the cardinal quadrants are pinnately arranged. Except for the long cardinal

septum the genus is identical with *Aulacophyllum*.

HALLIA VESICULATA Sloss, n. sp.

Plate 12, figures 1–16, text figure 3

External characters: Corallum simple, trochoid, curved ceratoid to cylindrical, typical trochoid specimens measure 50 mm high, 55 mm in diameter. Typical ceratoid

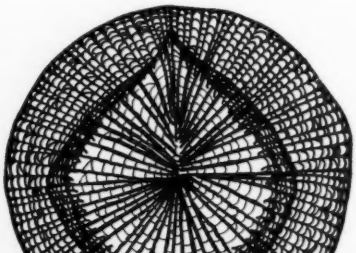


FIG. 3.—*Hallia vesiculata* Sloss, n. sp. Diagrammatic transverse section, ×1⅓.

specimens 80 mm high, 45 mm in diameter. One cylindrical specimen 150 mm by 50 mm. Epitheca thin, with well developed growth rings, calyx deep, paraboloid, with a narrow, shallow cardinal fossula about which septa of cardinal quadrants are pinnately arranged. Calicular edges of septa denticulate; denticulations correspond to slight undulations, which traverse septa at right angles to their calicular edges.

Transverse section: Fifty to 56 major septa, those of cardinal quadrants pinnately arranged to converge upon a long, persistent cardinal septum. Septa of counter quadrants radially arranged. Pinnate symmetry best developed in neanic stage, later obscured by secondary radiality. Minor septa extend one-half to three-quarters the distance to the axis, are contratingent (Smyth, 1937) in neanic stage, contraclined ephebically. Narrow pendant-shaped stereozone involving one or two rows of dissepiments present near the axial margin of the dissepimentarium, point of pendant being at cardinal septum. In some individuals the stereozone has accessory points at the alar septa, making it kite-shaped in outline. All septa slightly dilate within tabularium.

Longitudinal section: No tabulae, entire lumen occupied by undifferentiated dissepiments and tabellae arranged in closely spaced series of synclinal paraboloid curves. Where septa are essentially parallel to plane of section undulations appear as jagged serrations disposed like the carinae of *Heliophyllum*. Septal trabeculae appear as striations intimately associated with undulations on plane of septum.

Discussion.—This species appears to be close to "*Odontophyllum*" *convergens* (Hall) from the Sellersburg limestone of Indiana, but differs from that form externally in having a deeper calyx, a more shallow fossula, and a more erect corallum.

The most interesting feature of the species is the extreme variation in the shape of the corallum from trochoid or nearly turbinate forms to cylindrical shapes. The extremes of the variational series, trochoid and subcylindrical, appear to be more common than the intermediate shapes; originally therefore, it was thought possible to divide the species on this basis, but further examination of the material has revealed a complete, intergraded series. The occurrence in the same horizon at the same locality of varied shapes in the same species can not be explained wholly on the basis of environmental influence, for different shapes occur side by side in the shale. Wells (1937, p. 8), working on *Heliophyllum halli*, has indicated that the following factors may be operative:

1. Reproductive precocity.
2. Stability
   a. Stability: straight or regularly curved corallum.
   b. Instability: contortion of corallum.
3. Gerontism: gerontic contraction of corralum.
4. Irregularity of rejuvenescence.
5. Differential growth-rate
   a. Growth-rate of polyp faster than development of corallum: turbinate or patelliform.
   b. Variation in growth-rate of parts of polyp: reflexed calicular margin, or deep calicular pit.

Hallia vesiculata is a common coral in the Petoskey zone at Mud Lake and in the Potter Farm formation of the eastern area.

Type locality.—Petoskey zone, "Mud Lake" quarry, East Bay View, NE ¼ of NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich.

Other locality.—Grass roots and bed of small stream 1½ miles east of Bay View on U. S. Highway 31, 200 yards east of intersection of Michigan Highway 131. NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich.

Holotype.—Walker Museum, U. C. no. 38738.

HALLIA ZONATA Sloss, n. sp.

Plate 12, figures 17–21, text figure 4

External characters: Corallum simple, ceratoid, height of holotype, 75 mm; diameter at cardinal septum, 45 mm; diameter at alar septa, 38 mm. Calyx not fully known; apparently deep, paraboloid. Epitheca thin, ornamentation fine.

Transverse section: Ephebic stage: 46 major septa present. Cardinal septum persistent to axis, dilated by distal paliform lobe. Major septa of cardinal quadrants dilated from periphery to axis, pinnately arranged about cardinal septum; dilation confined to tabularium in counter quadrants. Minor septa contratingent, undilated. Dissepimentarium of counter quadrants bears U-shaped stereozone 2 mm wide, 1 mm from epitheca. Dissepiments numerous, fine, concentric.

Neanic stage: Only septa of cardinal quadrants markedly dilate. Subperipheral stereozone complete in all quadrants.

Longitudinal section: Dissepimentarium occupied by steeply dipping rows of numerous small globular dissepiments. Tabularium occupied by numerous small tabellae of uncertain orientation. Structures much obscured by dilate septa.

Discussion.—Although the species is known from only one specimen, it is felt that the characters are sufficiently distinct and peculiar to justify the establishment of a new species. The corals associated with the specimen are not markedly crushed except in the calicular portion; therefore it is assumed that the ellipsoid shape of the corallum is natural. The fact that the axes of the ellipse are oriented with the proto-septa of the coral is another point in favor of this argument.

Stereozones are characteristic of *Hallia* and *Aulacophyllum*, but the writer has not seen another coral with the peculiar pattern exhibited by this species. The neanic stage, however, exhibits a stereozone pattern quite similar to that seen in more common species of *Hallia* and *Aulacophyllum;* so it is probable that *H. zonata* represents an aberrant development of the trend.

Type locality.—Petoskey zone, "Mud Lake" quarry, East Bay View, NE ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich.

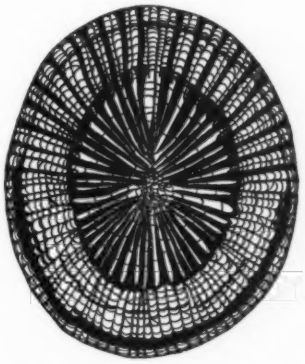


FIG. 4.—*Hallia zonata* Sloss, n. sp. Diagrammatic transverse section, ×1½.

Holotype.—Walker Museum. U. C. no. 38743.

Genus AULACOPHYLLUM Milne-Edwards and Haime, 1850

MILNE-EDWARDS and HAIME, *1850*, British Fossil Corals, p. lxvii.

Genotype, *Aulacophyllum sulcatum* (D'Orbigny).

Original description.—Polyp turbinate, solitary, subpedunculate; septa numerous, well developed; in one half the calyx they are regularly radiate, but in the other half they are separated into two fascicles by a long groove, at the bottom of which they almost cross in affecting a pinnate arrangement; no columella; tabulae poorly developed.

The principal character of the genus does not permit its confusion with any other cyathophylloid. (Translation from Milne-Edwards and Haime, 1851, p. 354.)

Discussion.—The close relationship beween *Hallia* and *Aulacophyllum* has already been discussed. It is probable that certain species that fall into one genus are more closely allied to species in the other than to forms which are placed with them in the same genus.

Simpson (1900, p. 210) withdrew certain species from *Aulacophyllum* into a new genus, *Odontophyllum*, on the basis of carinate septa. The genotype, *O. convergens*

(Hall), exhibits wavy septa like those of *Cymatelasma* Hill and Butler (1936, 516–527) and *Hallia vesiculata*, but this character is neither constant nor conspicuous nor is it diagnostic; therefore the writer does not consider *Odontophyllum* Simpson to be a valid genus.

Aulacophyllum is represented in the Traverse by one species in the Petoskey zone, two in the Gravel Point zone.

AULACOPHYLLUM BILATERALE Sloss, n. sp.

Plate 9, figures 18–20, text figure 5

External characters: Corallum simple, curved ceratoid. Holotype measures 30 mm in maximum diameter, 75 mm in height. Calyx and epitheca unknown.

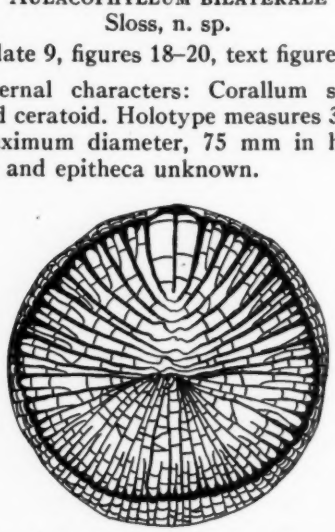


FIG. 5.—*Aulacophyllum bilaterale* Sloss, n. sp. Diagrammatic transverse section, ×1⅓.

Transverse section: Approximately 46 major septa present; arranged radially in counter quadrants, pinnately arranged about short undilated cardinal septum in cardinal quadrants. Major septa of cardinal quadrants markedly dilated within tabularium; their ends connected across cardinal loculus by fine wavy processes, which enclose a cardinal fossula. Minor septa extend over one half the distance from periphery to axis; contracline or contratingent in cardinal quadrants. Dissepimentarium bounded axially by a narrow stereozone formed by the dilation of inner ring of dissepiments.

Longitudinal section: No tabulae. Lumen occupied by undifferentiated dissepiments and tabellae which enclose larger vesicles on the cardinal than on the counter side but are nowhere arranged in order or series.

Discussion.—The species is known only from the holotype, a well-preserved specimen which adequately exhibits the specific characters.

There are some interesting changes exhibited during the ontogeny of the holotype. At a position 7 mm above the base of the corallum the dilated septa of the cardinal quadrants are crowded into about one quarter of the lumen, and the fossular structure is obscure. In the alar position there are three septa that appear to cross directly through the axis and are fused to the corresponding septa on the other side. At this stage there is a prominent peripheral stereozone. Twenty millimeters higher the full specific characters appear; the peripheral stereozone has migrated axially to bound the dissepimentarium; the fossulum is developed, and the reduction of the cardinal septum is evident. In the late ephebic or gerontic portion of the corallum, the specific characters are obscured by the diminished relative dilation of the septa and the appearance of a secondarily imposed radial symmetry, which replaces the pinnate arrangement.

The species differs from *Hallia vesiculata*, which it superficially resembles, by the reduction of the cardinal septum. From *Aulacophyllum hemicrassatum* it is distinguished by the lesser dilation of the septa. Nondilate septa in the counter quadrants separates the species from *A. mesodilatum*.

Type locality.—Grass roots and bed of small stream, 1½ miles east of Bay View on U. S. Highway 31, 200 yards east of intersection of Michigan Highway 131. NW ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich.

Holotype.—Walker Museum, U. C. no. 38710.

AULACOPHYLLUM HEMICRASSATUM Sloss, n. sp.

Plate 9, figures 9, 10, text figure 6

External characters: Corallum simple, curved trochoid. Holotype 40 mm in diameter, 45 mm high. Calyx deep, paraboloid not known in detail. Epitheca thin, exhibits growth annulations and septal grooves.

Transverse section: Forty-eight major septa; all but cardinal dilated within tabu-

larium, which is bounded by pendant-shaped stereozone; septa of cardinal quadrants much more highly dilated than those of counter quadrants, enclose fossulum occupied by short cardinal septum. Dissepimentarium confined to narrow peripheral band containing fine septa and numerous concentric dissepiments.

Longitudinal section: Tabularium largely occupied by dilated septa connected by a few short tabellae. Dissepimentarium appears 10 mm above base, does not become nver 3 mm wide.

Discussion.—This species appears to be quite close to *A. bilaterale*, differing from it in more marked septal dilation and shorter minor septa and correspondingly reduced dissepimentarium. *A. hemicrassatum* is an intermediate form between *A. bilaterale* and an undescribed species from the Jeffersonville limestone of Indiana, and the Davenport limestone of Vandruff's Island, Illinois. In the latter coral the septa of the cardinal quadrants are so dilated as to be laterally contiguous within the tabularium. Both the latter species approach *Papliophyllum elegantulum* Stumm (1937, p. 430) but differ from the Nevada form in lacking the peripheral dissepimental zone.

The species is known from a single specimen in the Gravel Point zone and from the Lower Ferron Point formation of Rockport, Alpena County, Mich.

Type locality.—Gravel Point zone, west end Petoskey Portland Cement Company quarry. SW ¼ sec. 2, T. 34 N., R. 6 W., Emmet County, Mich.

Holotype.—Walker Museum, U. C. no. 38709.

AULACOPHYLLUM MESODILATUM Sloss, n. sp.

Plate 9, figures 11–13

External characters: Corallum curved ceratoid, epitheca thin, bearing septal grooves and growth annulations. Diameter of holotype 55 mm at periphery of calyx, 70 mm high. Calyx cupshaped, 25 mm deep; walls descend abruptly from periphery, center occupied by low axial boss. Prominent cardinal fossulum placed at outside of curve of corallum. Septa of cardinal quadrants very thick, stand well above calicular floor pinnately arranged about fossulum. Septa of counter quadrants less prominent.

Transverse section: Forty-six major septa present, all heavily dilate within tabularium, those of cardinal quadrants more so than others. Cardinal septum extends about

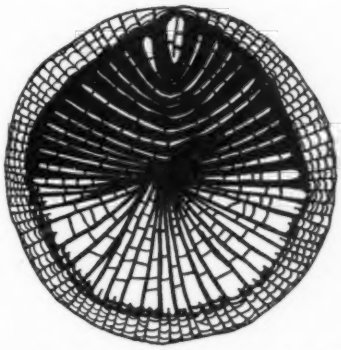


FIG. 6.—*Aulacophyllum hemicrassatum* Sloss, n. sp. Diagrammatic transverse section, ×2.

one half distance to axis; neighboring septa arranged pinnately, extend to axis. Septa of counter quadrants radially arranged near periphery, tend to become fasiculate at axial ends. Dissepimentarium restricted to peripheral 3 mm of lumen. Septa very fine within dissepimentarium, dissepiments concentric, numerous. Dissepimentarium bounded by ring of dilate dissepiments, beyond which minor septa extend but slightly.

Discussion.—This form is exceedingly close to, if not conspecific with, a form from the Cedar Valley (U. C. no. 25625). Both have dilate septa within the tabularium, and pinnate arrangement of the septa of the cardinal quadrants, but the Iowa form is smaller and has a wider dissepimentarium.

The species is known from a single well-preserved specimen collected from the "upper Blue shale" of the top of the Gravel Point stage.

Type locality.—Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich.

Holotype.—Walker Museum, U. C. no. 38704.

Genus DIVERSOPHYLLUM Sloss, n. gen.

Genotype, *Diversophyllum traversense* (Winchell).

Cylindrical or ceratoid simple rugose corals with long, unornamented septa, and vertically elongate concentric dissepiments; tabulae flat or domed, often incomplete but not commonly differentiated; septa characteristically exhibiting gerontic lonsdaleoid retreat.

Genus differs from *Tabulophyllum* Fenton and Fenton (1923, p. 30) in exhibiting definite and persistent minor septa, from *Diphyphyllum* Lonsdale (1845, p. 622) and *Diphystrotion* Smith and Lang (1930, pp. 177–199) in solitary habit.

Discussion.—The type species exhibits such extreme variation in external shape and internal structure that the relationships of the genus are not readily apparent. One end of the variational series is represented by a ceratoid form with flat tabulae and numerous inclined dissepimental rows as in *Campophyllum* Milne-Edwards and Haime; at the other end of the series are attenuate cylindrical corals with reduced dissepimentaria and highly arched tabulae. Inasmuch as certain large specimens exhibit flat tabulae and wide dissepimentaria in the ephebic portion of the coralla and arched tabulae with restricted dissepimentaria neanically, it is felt that the latter condition is of greater phylogenetic significance. Small cylindrical specimens and immature stages of large ceratoid specimens exhibit many points in common with genomorphic forms of *Lithostrotion* Fleming described by Smith and Lang.

The genus *Tabulophyllum* Fenton and Fenton has been made the repository of a variety of corals of different affinities. As defined by the genotypic species, *T. rectum* Fenton and Fenton, the genus may include only those species that have irregular, reduced, or rudimentary minor septa. It is possible that *T. ehlersi* Fenton and Fenton and *T. rotundum* Fenton and Fenton are referable to *Diversophyllum*. Without taking account of possible convergence *Tabulophyllum* and *Diversophyllum* appear closely related. Both have long major septa, longitudinally attenuate dissepiments, and exhibit a lonsdaleoid trend. However, *Tabulophyllum* does not seem to play any part in the phylogenesis of Carboniferous genera; it seems, instead, to represent a degeneracy of the *Diversophyllum* stock.

DIVERSOPHYLLUM TRAVERSENSE (Winchell)

Plate 11, figures 13–23; plate 12, figure 22, text figure 7

Zaphrentis traversensis WINCHELL, *1866*, The Grand Tranverse Region, p. 90.

Cyathophyllum houghtoni ROMINGER, *1876*, Michigan Geol. Survey, vol. 3, pt. 2, p. 104; *Not* HALL, *1876*, III. Devonian Fossils (Albany: Weed, Parsons and Company), vol. XXX, figs. 1–2.

Tabulophyllum houghtoni FENTON and FENTON, *1923*, "Hackberry stage," Michigan, Univ., Mus. Geology, Contr., vol. 1, p. 31.

Original description.—Fossette rudimentary. Differs from *Cyathophyllum simplex* Hall in its more abundant epitheca, less contorted lamellae, its finely vesicular outer zone, and its more elongated and erect form. Often attached obliquely (Winchell, 1866, p. 90).

External characters: Corallum simple, cylindrical to ceratoid, one specimen exhibiting increase by lateral gemmation. Average ceratoid specimen measures 30 mm in greatest diameter, 75 mm in height; average cylindrical specimen 15 mm by 75 mm. Largest specimen discovered measures 33 mm by 150 mm. Epitheca thick, lacks septal grooves, bears deep growth constrictions. Periodic rejuvenation characteristic, leaves edges of abandoned calices protruding around corallum as series of sharp, upturned, frill-like ridges. Calyx depth about equal to radius, walls steeply dipping to domed, flat, or slightly concave floor, which may exhibit a low axial boss or shallow axial pit. Several major septa extend to axis, meet without torsion or formation of axial complex.

Transverse section: Thirty-two to 34 major septa extend from peripheral stereozone of variable width, either anastomose subaxially or extend to axis. Minor septa extend at least one-half distance to axis in ephebic sections of ceratoid coralla, restricted or lacking in neanic sections of cylindrical coralla. Gerontic sections of large coralla exhibit lonsdaleoid withdrawal of septa from periphery and replacement by large dissepiments. Dissepiments characteristically few, seldom arranged in more than three concentric rings. Peripheral stereozone often repeated within lumen by rejuvenation.

Longitudinal section: Thin cylindrical specimens lack dissepimentarium in neanic

stage, never develop more than two steeply inclined rows of large, elongate dissepiments. Ceratoid specimens develop several axially inclined rows of dissepiments, which may occupy over half the lumen. Peripheral stereozone often involved with dissepimentary rows as result of rejuvenation. Tabulae highly domed in thin cylindrical coralla, less domed in subcylindrical coralla, flat or slightly concave in ceratoid specimens. Large subcylindrical coralla exhibit domed neanic tabulae, flat ephebic tabulae. Tabulae commonly incomplete, rarely differentiated. Some septa that do not extend to axis along whole of their distal ends have axial ridgelike processes on top of tabulae (like amplexoid septa), appear in median section as spines on tabulae.

Discussion.—Winchell's inadequate original description of the species was supposed to be followed by figures. The figures were prepared but never published; they are now at the University of Michigan, where Dr. G. M. Ehlers has compared them with Winchell's specimens in the collections of Alma College and has been able to recognize the figured specimens. One of the figures bears the inscription "type" in Winchell's handwriting. Whether this unpublished designation suffices to make the specimen the holotype or whether it should be considered a lectotype designated by the present writer is an academic question of no real importance. The specimen is an asymmetrically cut longitudinal section with half a transverse section shown on one end. Dr. Ehlers has found the other half of the specimen in the University of Michigan collections, and from the two halves the specific characters can be made out. The specimen is an intermediate type with slightly domed tabulae, rather short minor septa, and a dissepimentarium restricted to the peripheral one-third of the lumen.

The writer has compared *Diversophyllum traversense* (Winchell, 1866) with the types of *Cyathophyllum houghtoni* Rominger, 1876, and found the latter to be a synonym. The distinction between *Diversophyllum* and *Tabulophyllum* Fenton and Fenton has already been discussed.

It may be demonstrated that there is a complete intergradation between specimens with ceratoid and cylindrical coralla, flat tabulae and arched tabulae, wide dissepimentaria and restricted dissepimentaria, long minors and short minors. It is more difficult, however, to explain why this variation exists. Wells (1937) has suggested that

FIG. 7.—*Diversophyllum traversense* (Winchell). *A*, *B*, Diagrammatic longitudinal and transverse sections of a specimen exhibiting domed tabulae and a restricted dissepimentarium, ×1½; *C*, diagrammatic longitudinal section of a specimen with flat tabulae and a wide dissepimentarium, ×1½.

broadly conical forms of *Heliophyllum halli* are the result of differential growth rate, the polyp growing faster than the corallum, but the reasons for the differential growth rate are not made clear. It seems possible that in the teeming habitat of a bioherm some individuals might be crowded so that certain structures would become reduced and others warped to allow the function of the polyp to proceed. The fact that the coralla are not polygonal does not exclude the possibility of crowding by soft-bodied organisms. Moreover, at locality 1, in the "upper Blue shale," which carries an exceptionally rich fauna characterized by a profusion of encrusting forms and many large colonies of *Prismatophyllum*, thin cylindrical specimens of *Diversophyllum* are common; whereas at locality 5 the species occurs in a different facies, which does not bear so abundant a fauna, the species attains great size, and small cylindrical forms are unknown.

The species has been recognized by the writer as occurring in the Upper Alpena limestone of the eastern side of the Peninsula, the Cedar Valley formation of Iowa, and the limestones of Hay River, Northwest Territory, Canada.

Type locality.—Winchell's (1866) locality number 861b, NW ¼ sec. 2, T. 34 N., R. 6 W. The specimens were probably collected from low cliffs on the lake shore near the present site of the Petoskey Portland Cement quarry. The horizon was probably in the upper part of the Gravel Point zone, possibly the "lower Blue shale."

Other localities.—Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich.

West end Petoskey Cement Company quarry. SW ¼ sec. 2, T. 34 N., R. 6 W., Emmet County, Mich.

Holotype.—One half at Alma College, Michigan (Winchell's no. 2720); one half at University of Michigan, Ann Arbor.

Genus DISPHYLLUM de Fromentel, 1861

DE FROMENTEL, *1861*, Introduction a l'Etude des Polypes Fossiles, Paris, p. 302; revised by LANG and SMITH, *1935*, Geol. Soc. London Quart. Jour., vol. 91, p. 544.

Genotype, *Disphyllum caespitosum* (Goldfuss), by subsequent designation (Lang and Smith, 1934, p. 78).

Revised diagnosis.—Phacelloid rugose corals in which increase may be lateral or calicular; the septa rarely reach the axis, but are usually long and typically thin; the tabulae are sometimes complete, though generally incomplete and differentiated into a transverse axial and an inclined periaxial series; with dissepiments typically small, strongly arched, sometimes of one, but frequently of two, kinds: an inner, single series of globose, distally directed dissepiments, and an outer series of flat or arched dissepiments (Lang and Smith, 1935, p. 545).

Discussion.—Lang and Smith have lumped nine genera into *Disphyllum* and have clarified the confused situation surrounding *Cyathophyllum caespitosum* Goldfuss. It seems possible to the writer that the simplification has been carried too far so as to include some obviously unrelated species in the same genus. A division based on the differentiation of dissepiments and tabulae would be logical, but until the relationships are more clearly understood it is probably better to retain the simplified classification. The present conception of this genus again serves to illustrate the doubtful value of colony form as a generic character.

DISPHYLLUM PANICUM (Winchell)
Plate 9, figures 25–27

Cyathophyllum panicum WINCHELL, *1866*, The Grand Traverse Region, p. 90.

Diphyphyllum panicum ROMINGER, *1876*, Michigan, Geol. Survey, vol. 3, pt. 2, p. 125, pl. 47, fig. 3.

Diplophyllum panicum GRABAU and SHIMER, *1909*, North American Index Fossils, vol. 1, p. 75.

Cylindrophyllum panicum EHLERS and WHITE, *1932*, Michigan, Univ., Mus. Paleont., Contr., vol. 4, p. 93.

Discussion.—Ehlers and White have published adequate description and figures of the species and very logically referred it to *Cylindrophyllum* Simpson. Lang and Smith (1935, p. 544) consider *Cylindrophyllum* to be synonymous with *Disphyllum*, so the species *panicum* is referred to the latter genus. Species that have been placed in *Cylindrophyllum* differ from the genotype of *Disphyllum* in that they lack differentiated tabulae and dissepiments. It is possible that further study will show that *Cylindrophyllum* should be reinstated.

Ehlers and White (1935, p. 97) have described a species from the Potter Farm formation at Alpena as *Cylindrophyllum hindshawi*. In the opinion of the writer this form should be considered a variant of *D. panicum* rather than a distinct species.

According to Ehlers and White typical examples of the species are also found in the Potter Farm formation indicating a close relationship between the faunas of the Potter Farm formation and Petoskey zone.

Localities.—Specimens in the Walker Museum collection are from the following localities:

Petoskey zone, "Mud Lake" quarry, East Bay View (Kegomic), NE ¼ of NW ¼ sec. 34. T. 35 N., R. 5 W., Emmet County, Mich.

Petoskey zone, Northern Lime and Stone Company quarry, Petoskey, NE ¼ sec. 32, T. 35 N., R. 5 W., Emmet County, Mich.

Type material.—The holotype is possibly at Alma College, Mich. Other material collected by Winchell and specimens figured by Rominger are at the University of Michigan, Ann Arbor. Comparative material collected by the writer is at Walker Museum, University of Chicago.

Genus PRISMATOPHYLLUM Simpson, 1900

Genotype, *Prismatophyllum prisma* Lang and Smith, 1935, Geol. Soc. London Quart. Jour., vol. 91, p. 558; *P. rugosum* Simpson, *1900*, New York State Mus. Bull., vol. 8, p. 218.

Revised description.—Cerioid rugose corals with septa that may or may not reach the axis; tabulae typically differentiated into a horizontally disposed axial series and an axially inclined periaxial series; and typically numerous, small, globose dissepiments. (Lang and Smith, 1935, p. 559.)

Discussion.—The genus has been involved in nomenclatorial difficulties due to the fact that Milne-Edwards and Haime in describing "*Cyathophyllum rugosum*" wrongly thought they were dealing with "*Astrea rugosa*" Hall. Therefore when Simpson erected the genus *Prismatophyllum* on Milne-Edwards and Haime's "*rugosum*" he used a homonym for the genotype. This confusion has been cleared by Lang and Smith (1935, pp. 538–590) who renamed the genotype *Prismatophyllum prisma*.

Lang and Smith discuss *Prismatophyllum* as a logical link between the phacelloid *Disphyllum* and the plocoid *Phillipsastrea*. Traverse species of *Prismatophyllum* commonly have individuals within a colony or portions of cerioid colonies that exhibit a phacelloid trend. This variation may be induced by environmental stimuli. T. W. Vaughan (1917, p. 202) has shown that on modern coral reefs the species inhabiting the lagoons are dendroid or phacelloid, whereas those on the sea slope are cerioid or plocoid. He explains that, under lagoonal conditions of heavy sedimentation and turbid water, the cerioid and plocoid forms, with their wide horizontal surfaces, offer great areas for burial by sediment. Thus they might not survive, although dendroid and phacelloid colonies would live since the separate individuals would gather little sediment. Thus it is possible to account for the shifting in the colony form of one species from cerioid to phacelloid purely as the result of environmental stimuli. It is, however, harder to envisage a variation in the direction of plocoid colonies in which the septa of adjoining individuals are confluent, for in the most compactly cerioid colony of *Prismatophyllum* the septa of one individual usually meet an interseptal loculus of the adjoining corallite, and the bounding wall is always definitely marked.

The genus also appears closely related to *Acervularia* Schweigger, differing from that genus in the lack of an aulos and the character of the tabulae. Certain species of *Prismatophyllum* exhibit dilate dissepiments and carinae at the axial boundary of the dissepimentarium and in this manner approach the condition of *Acervularia*.

Another possible, though obscure, relationship is with the common solitary form *Heliophyllum*. Both genera are characterized by small globose dissepiments, incomplete tabulae, and prominent arched carinae. Other members of the group, such as *Disphyllum*, *Lithostrotion*, and *Phillipsastrea*, have recognizable solitary relatives, but many forms of *Heliophyllum* increase by lateral and parricidal gemmation, a character indicative of colonial relationship.

PRISMATOPHYLLUM PERCARINATUM
Sloss, n. sp.

Plate 10, figures 6–9

External characters: Cerioid corals typically forming broad, flat, or dorsally convex colonies arising from a central point of attachment. Under side bears a thin annularly wrinkled holotheca with fine septal

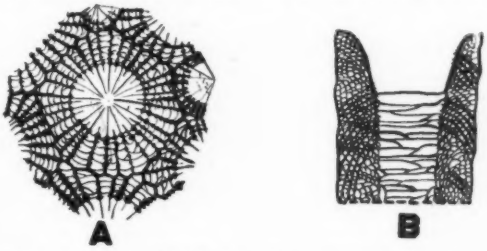


FIG. 8.—*Prismatophyllum percarinatum* Sloss, n. sp. *A*, Diagrammatic transverse section, ×2; *B*, diagrammatic longitudinal section, ×2.

grooves. Colonies may attain 30 cm in diameter, are commonly 12 to 16 cm. Individual adult corallites polygonal, average 10 mm in mean diameter. Immature individuals commonly circular in outline. Some colonies bear individuals protruding above general surface or projecting from edge, in which case these individuals are circular in cross-section and phacelloid in their relation to neighboring corallites.

Calices extremely variable, being different in form between colonies or between individuals of the same colony. Most frequently occurring calyx type bears horizontal peripheral platform occupying one half the radius, a deep calicular pit at the axis. All degrees occur between this central type and forms in which the calicular wall descends

abruptly from periphery as in *P. profundum* (Hall and Whitfield). Ephebic calices bear edges of 38 to 40 denticulate, highly carinate septa. Majors and minors not differentiated near periphery; septa taper axially, majors extending close to axis.

Transverse section: Dissepimentarium occupies one-half the radius, bounded axially by large carinae, occasionally by dilate dissepiments, to form a discontinuous wall similar to, but not homologous with, aulos of *Acervularia* Schweigger (Smith and Lang, 1931, p. 85). Major septa approach but do not attain axis, minor septa extend but slightly beyond dissepimentarium. All septa dilate, carinate within dissepimentarium; fine, unornamented within tabularium. Character of carinae variable; three types may occur in one individual—large diamond-shaped areas, simple yard-arms (Hill, 1935, p. 501), or prolongations of angles of "zig-zag septa" (Hill and Butler, 1936, p. 523). Dissepiments concentric, numerous, fine. Boundary between individuals fine but distinct.

Longitudinal section: Numerous small globose dissepiments arranged in rows, which vary in same manner as calicular platform. Rows may be horizontal at periphery, descend abruptly at margin of dissepimentarium, or descend directly from periphery. Dissepimentarium restricted in neanic stage, quickly widens to occupy one-half the lumen in ephebic stage. Tabulae numerous, horizontal, complete or incomplete, not differentiated, Arched carinae, spaced approximately 0.3 mm apart, prominent wherever plane of section transects plane of septum, and extending but slightly into tabularium.

Discussion.—Prismatophyllum percarinatum is the coral of the familiar "Petoskey stone" of northern Michigan. It has been identified by most workers in the area as *P. davidsoni* (Milne-Edwards and Haime) but it has been shown (Stewart, 1938, p. 53) that specimens of the latter species from the accepted type locality in France do not exhibit carinae. The aulos-like character of the boundary of the dissepimentarium gives the species the appearance of an *Acervularia*, but it differs from that genus as redefined (Smith and Lang, 1931, p. 85) in lacking differentiated tabulae and possessing numerous dissepiments. The species differs from *P. profundum* and *P. inequalis* of the Iowa Devonian, for these forms have domed axial, horizontal periaxial tabulae and lack dilate septa. There are many points in common between *P. percarinatum* and *P. whitfieldi* Stewart (1938, p. 52) from the Columbus limestone of Ohio, but the Michigan species differs widely from the Ohio species in colony form, has a larger number of septa per corallite, lacks the joining of major septa at the axis, has more horizontal, more commonly complete tabulae, and smaller, more numerous dissepiments.

P. percarinatum occurs in great abundance in the calcareous shales of the Gravel Point zone, in which colonies of all sizes are among the most common fossils.

Type locality.—Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich.

Holotype.—Walker Museum, U. C. no. 38746.

PRISMATOPHYLLUM PAUCISEPTATUM Sloss, n. sp.

Plate 10, figures 10–13

External characters: Subcerioid corals forming spheroidal masses, which arise from a central point of attachment. Individuals on lower side of colony intersect surface at a low angle. Elsewhere individuals intersect surface at right angles. No holotheca present. Individuals phacelloid to cerioid in relation to one another. Some circular in cross-section, barely touch neighboring corallites; others are polygonal, in contact with adjacent corallites at all points on periphery. Sections through interior of colony indicate that relation is cerioid below surface, a condition difficult of explanation in view of absence of secondary tissue between individuals.

Ephebic corallites average 18 mm in diameter. Depth of calyx approximately one-half diameter; calicular walls descend abruptly from periphery to flat floor occupying two thirds the diameter. Many individuals exhibit calicular rejuvenation. Septa short, thick, widely spaced, coarsely carinate and denticulate. Minor septa rarely apparent.

Transverse section: Sixteen to 18 tapering

major septa of unequal length present in ephebic stage. Few septa approach axis, most restricted to peripheral two-thirds of lumen. Septa slightly dilate, commonly "zig-zag," ornamented with diamond-shaped carinae within dissepimentarium; thin, wavering, unornamented in tabularium. In neanic stage major septa persistent to axis, minors short but prominent. Amplexoid retreat of both series marked in ephebic stage. Minors commonly lacking in late ephebic or gerontic stage. Dissepiments numerous, restricted to narrow peripheral border, concentric if minor septa are present, herring-bone if minors are absent.

Longitudinal section: Dissepimentarium restricted to within 2.5 mm of border. Dissepiments numerous, globular, arranged in subvertical rows. Tabulae numerous, incomplete but not differentiated, commonly horizontal, occasionally domed or sagging. Arched carinae spaced approximately 0.6 mm apart; carinae not prominent.

Discussion.—The taxonomic position of this species is in doubt because its colonial form places it as an intermediate type between the phacelloid *Disphyllum* and the cerioid *Prismatophyllum.* At present, in view of the preponderance of polygonal corallites it seems best to consider the species as an aberrant amplexoid *Prismatophyllum* and wait for the discovery of more specimens to indicate the true generic affinity.

The species serves admirably to point out the artificial nature of the criteria used for generic distinction among the compound corals. At present the corals of the group under discussion are called *Disphyllum* if they are phacelloid, *Prismatophyllum* if cerioid, *Phillipsastrea* if plocoid, or *Macgeea* if solitary. It has been shown that a single species may vary so widely under the influence of environmental stimuli as to fall into two or more of these artificial categories. Moreover, it is likely that each "genus" contains forms of varied origin. Under the same ecologic conditions corals of widely separated stocks would tend to build colonial structures of similar form and thus would be included in the same "genus." It is hoped that after many more detailed studies of the internal structures of the individuals of colonial type have been made, the true relationships will appear. Then the taxonomy may be based upon the morphology of the individual, and the differences in colonial habit will be reduced to varietal significance. Unfortunately the present state of knowledge will not permit such a rearrangement, and an attempt would only lead to further confusion.

P. pauciseptatum is known from one large colony from the float of the Petoskey zone at East Bay View.

Type locality.—"Mud Lake" quarry, East Bay View (Kegomic), NE ¼ sec. 34, T. 35 N., R. 5 W., Emmet County, Mich.

Holotype.—Walker Museum, U. C. no. 38752.

PRISMATOPHYLLUM CRISTATUM (Rominger)

Plate 10, figures 1–5

Cyathophyllum cristatum ROMINGER, *1876,* Michigan Geol. Survey, vol. 3, pt. 2, p. 108.

External characters: Cerioid corals with polygonal ephebic individuals averaging approximately 17 mm in mean diameter; small, immature individuals round in cross-section. Calices typically exhibit narrow horizontal calicular platform and deep, cup-shaped calicular pit. Major septa approximately 20 in number, carinate and denticulate, approach axis on floor of calicular pit. Minor septa finely carinate, do not extend beyond calicular platform.

Transverse section: Major septa approach close to axis in neanic and early ephebic stages, retract toward periphery gerontically. Majors markedly dilate within dissepimentarium, taper to fine line in tabularium. Carinae not prominent. Minor septa extend not over one-third distance to axis. Dissepiments numerous, concentric to herring-bone in pattern.

Longitudinal section: Dissepiments numerous, small, globular, arranged in steeply inclined rows. Tabulae closely spaced, horizontal, commonly incomplete but not differentiated. Carinae not prominent, closely spaced.

Discussion.—This species, although much larger, appears in transverse section and calicular view to be quite similar to *P. percarinatum;* both species have horizontal calicular platforms and dilate septa within the dissepimentarium. *P. cristatum* differs

from *P. percarinatum*, however, in having a restricted dissepimentarium, amplexoid septa, and in lacking well-developed carinae —all interpreted as evidence of degeneracy. From *P. pauciseptatum*, which it closely resembles in longitudinal section, the species is distinct by reason of the smaller dissepiments, more closely spaced tabulae, more numerous septa, better-developed minor septa, and constant cerioid form.

Rominger's holotype is an execrable specimen, a fragment of a colony with no calices preserved. The specific characters are clearly visible, however, and the discovery of two more specimens has made a redefinition of the species possible.

Type locality.—Rominger gives no specific locality, merely stating that the species "occurs rarely in the strata of Little Traverse Bay." It is probable that he collected his specimens from the now-covered lake bluff outcrops of the Gravel Point zone at the mouth of Bear Creek, where the town of Petoskey now stands.

The two hypotypes were all collected by Mr. A. W. Slocom at the following locality:

Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich.

Type material.—The holotype is at the University of Michigan, no. 5322, where also is deposited one of the hypotypes. One hypotype is at Walker Museum, University of Chicago.

PRISMATOPHYLLUM CRISTATUM MICROCARINATUM Sloss, n. var.

Plate 10, figure 14

External characters: Dimensions and manner of growth as in *P. cristatum*. Calicular walls descend abruptly from periphery to deep calicular pit. Septa prominent, fine, occasionally exhibit very fine, barely visible carinae.

Transverse section: Differs from *P. cristatum* in lack of septal dilation and apparent carinae, otherwise similar.

Longitudinal section: Differs from *P. cristatum* in lack of apparent carinae, otherwise similar.

Discussion.—The variety exhibits the bell-shaped calices described by Rominger, but, as the internal structure does not fit that of Rominger's type specimen, a distinction has been made on the basis of the differences outlined above. It is possible that further study will show that the variety should be given specific status; the two forms are quite easily separated by external characters, but as has been indicated elsewhere such characters are not wholly trustworthy.

Rominger, working with poorly preserved material, evidently confused the two forms (they occur in the same beds) as his original description mentions characters found in both forms.

Type locality.—Bell quarry, 2.3 miles east of Charlevoix County line on U. S. Highway 31. NE ¼ sec. 8, T. 34 N., R. 6 W., Emmet County, Mich.

Type.—Walker Museum, University of Chicago, U. C. no. 18402.

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JOURNAL OF PALEONTOLOGY, VOL. 13, NO. 1, PP. 74–76, 6 TEXT FIGS., JANUARY, 1939

AN ORDOVICIAN ZITTELOCERAS FROM WISCONSIN

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ABSTRACT—An external mold of *Zitteloceras clarkeanum* Foerste, from the Mid-Ordovician Platteville formation of Wisconsin is described and compared with the holotype. Some features of ornamentation, well shown by this specimen, are scarcely discernible on the poorly preserved holotype, the only other recorded individual of the species. Particularly striking are the frilled lirae which, at the aperture, rise above the general surface at an angle of about 55° and to a height of 5 or 6 millimeters.

A FRAGMENT of an external mold of *Zitteloceras* Hyatt recently found in Lower Platteville beds of the Middle Ordovician of Wisconsin is unique in its excellent preservation of details of ornamentation seldom shown by specimens of the genus.

The specimen is herein described in the belief that its description will constitute a contribution to the limited knowledge of the characters of *Zitteloceras* and will add something to the understanding of the species *Z. clarkeanum*, with which the specimen is evidently conspecific. Direct comparison with the holotype of *Z. clarkeanum* has been made, but unfortunately the ornamentation is very poorly shown in that individual, whereas the specimen at hand is lacking in some of the features by which *Z. clarkeanum* was first made known.

The fragment was found in the mantle rock at West Blue Mound, about 25 miles west of Madison, in the Driftless Area of Wisconsin. Although the horizon from which it came is not known with certainty, it is lithologically like the Pecatonica and Mifflin beds of the Platteville formation.

The writer is indebted to Profs. W. H. Twenhofel and N. D. Newell for helpful criticisms and suggestions, and to Prof. C. R. Stauffer of the University of Minnesota, who kindly loaned the holotype of *Z. clarkeanum* for study.

SYSTEMATIC DESCRIPTION

Genus ZITTELOCERAS Hyatt, 1884

ZITTELOCERAS CLARKEANUM Foerste

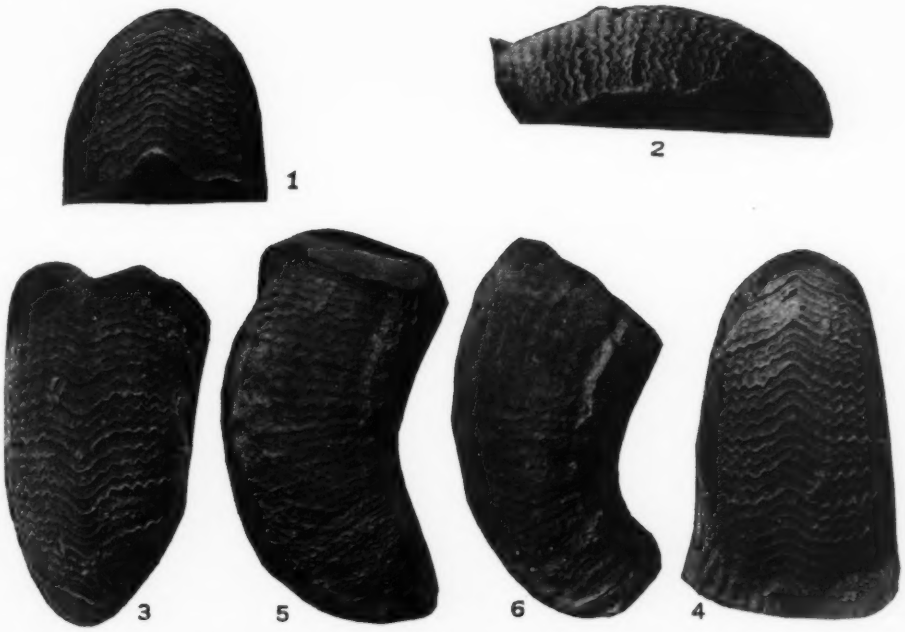
Text figures 1–6

Cyrtoceras hallianum Clarke, *1887*, Geology of Minnesota, vol. 3, pt. 2, p. 805, pl. 60, figs. 11, 12.

Zitteloceras clarkeanum Foerste, *1917*, Cinn. Soc. Nat. Hist., Jour., vol. 22, p. 52; *1933*, Denison Univ., Sci. Lab., Jour., vol. 28, pp. 83, 84, pl. 27, figs. 6*a–d*.

The holotype consists of a distorted internal mold, on which has been superposed part of the external ornamentation, and a roughened, poorly preserved external mold, which scarcely gives an adequate conception of the surface ornamentation. Foerste (1) described the type in 1933 as follows:

> Specimen 60 mm in length measured along its convex ventral outline. The radius of curvature of this outline varies from 30 mm along the phragmacone to about 35 mm along the living chamber. The dorsoventral diameter of the conch increases from 16.6 mm near the lower end of the specimen to 24 mm at a point 33 mm farther up, when measured along its ventral outline, and to 25.5 mm at the top of the specimen after an additional interval of 25 mm. Originally the cross-section of the conch probably was almost circular, as in other species of this genus. At present, however, it is strongly compressed, its lateral diameter being estimated at 21 mm where its dorsoventral diameter is 25.5 mm. Of the living chamber a length of 25 mm is preserved ventrally, and 17 mm dorsally. Where its dorsoventral diameter is 21 mm, 6 camerae occur in a corresponding length when counted along its ventral outline immediately beneath. Along the lower part of the specimen the sutures of the septa rise moderately in a ventral direction, but on approaching the upper part of the phragmacone these sutures rise at an increasing rate until at the base of the living chamber they form an angle of 10° with a transverse plane. The course of these sutures is almost straight, curving only faintly downward along the lateral sides of the conch. The siphuncle is very close to the ventral wall of the conch but is not known to be in actual contact with the latter. The surface of the shell is ornamented by sinuous striae, whose crests project slightly in a lamellose manner. About 5



FIGS. *1–6.—Zitteloceras clarkeanum* Foerste. *1*, A ventral profile view of a clay impression of the specimen from West Blue Mound, Wisconsin; it is now no. 20384 in the collection of the Geological Museum of the University of Wisconsin. *2*, A longitudinal profile view. *3*, A ventral view of the same specimen, showing the regularly frilled lirae, and the longitudinal ridges which they form. *4*, The same specimen, inverted, but lighted to show more clearly the lira forming the apertural margin. *5*, A lateral view of the holotype, a mold of the interior of the conch; several sutures are plainly seen, as well as some lirae, which have been superposed on it by the external mold; the position of the living chamber is not indicated by the oblique crack running across the shell, as mistaken by Foerste, but by the most adapertural suture; this specimen was collected at Janesville, Wisconsin, by Charles Schuchert and is no. 4120 in the Univ. of Minnesota collection. *6*, A lateral view of a clay impression of a mold of the exterior of the same specimen showing more clearly the external ornamentation.

of these striae occur in a length of 5 mm where the dorsoventral diameter of the specimen is 22 mm, if counted along its ventral outline. The undulations of these transverse striae are conspicuous, about 5 downward deflections occurring in a width of 10 mm, at the diameter mentioned. The general course of these undulating striae is almost directly transverse to the curving vertical axis of the conch, but along the median part of its ventral side they curve rather abruptly downward for a width of 7 mm and a depth of fully 2 mm or slightly more. This indicates the presence of a sharply defined hyponomic sinus at various stages of growth of the conch.

As previously mentioned the specimen from Blue Mound is an external mold of the ventral and apertural end of the conch. It is cyrtoconic and measures about 55 mm along the middle of the venter, the original length, however, having been somewhat greater. The radius of curvature, measured by plotting the outline of an artificial cast and then determining the radius of the circle which it most closely approximates, averages about 25 mm. The lateral diameter can only be measured with certainty over the last 30 mm of the shell in an adapertural direction; the greatest lateral diameter, at the aperture, is 27 mm; 30 mm back of the aperture the diameter is 23 mm, the change in width of the shell being very gradual. The dorsoventral diameter cannot be measured directly, but can be estimated where the lateral diameter is 26 mm. Here the walls of the artificial cast begin to curve inward, as would be expected along the circumference of a circle when one-half has been completed. The dorsoventral measure-

ment obtained in this way is 28 mm, or 14 by 2, which indicates that the conch is approximately circular in cross section.

Since the fragment is an external mold neither the septal characters, nor the position of the siphuncle, are shown.

The surface of the shell is ornamented by parallel raised ridges or lirae, called striae by Foerste, which are nowhere straight but are regularly sinuous, crossing the conch transversely. These are spaced 3 to 4 in a distance of 5 mm along the mid-line of the venter, and are more closely crowded toward the apical end. The crenulations of the lirae are subangular and closely spaced; 5 to 7 crests occur in a width of 10 mm measured along the lirae. Since the lirae are parallel throughout their sinuous course, the crests and sinuses of adjoining lirae are lined up longitudinally so as to give the appearance of longitudinal ridges. This feature is also observable on the holotype. The lirae appear to be of two orders of size. Coarse lirae are separated from each other by finer and less conspicuous lirae. Each coarse lira is separated from the preceding fine lira by a somewhat wider interval than the spaces between the finer lirae. The coarse lirae are spaced about 8 mm apart, measured along the midventral line and are separated by three or four fine lirae; at a distance of about 20 mm from the adapertural end the spacing of the coarse lirae abruptly decreases to about 5 mm, and the number of intervening lirae decreases to one or two. It is possible that this change is indicative of the change from youth to maturity.

The hyponomic sinus may be seen at the aperture and is indicated on the general shell surface by a downward deflection of the lirae along the median line of the venter. The sinus thus formed by each lira is about 5 mm in width and about 2 mm in length.

The most unusual feature of the lirae is their height above the general shell surface, for at the aperture near the lateral margin the last lira flares at an angle of approximately 55° 5 to 6 mm above the general shell surface. At the hyponomic sinus this angle becomes about 90°, a modification probably allowing for greater freedom of the hyponome. It is probable that the earlier lirae rose an equal distance above the shell surface, but because of the nature of the specimen this can only be inferred.

Similar lirae have been described on only one other specimen to the writer's knowledge. This was described by M. Fritz (2) as *Zitteloceras fimbriatum*. Whether or not such projecting lamellose lirae occurred on all species of the genus is difficult to say; it is likely that such lirae would very easily escape preservation.

Remarks.—As seen through a comparison of the above descriptions, the specimen from Blue Mound differs from the holotype in certain respects. The type is somewhat smaller, but no evidence has been found indicating that either specimen had reached its full growth; it is possible that a slight adapertural straightening of the lirae on the type may indicate maturity, but this may also be due to imperfect preservation; the change in the spacing of the coarser lirae on the specimen from Blue Mound may also be an indication of maturity, but it is by no means a certain criterion. The radius of curvature of the type appears to be somewhat greater than in the present specimen, and its lirae are more closely spaced. The lirae of the specimen from Blue Mound have subangular crests and sinuses, whereas those of the type are more gently sinuous, but this may be merely an individual variation. No evidence is found on the type indicating that the lirae are higher than 0.5 mm above the general shell surface, but this again may be due to faulty preservation.

The specimen from Blue Mound also shows some resemblance to *Z. hallianum* D'Orbigny, particularly in the presence of regularly frilled lirae. However, the latter species is very much smaller, a mature specimen being only 23 mm long, and its lirae are more rounded and more closely crowded.

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JOURNAL OF PALEONTOLOGY, VOL. 13, NO. 1, PP. 77–79, JANUARY, 1939

ATURIAS FROM THE EOCENE OF PANAMA

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ABSTRACT—*Aturia peruviana* Olsson is illustrated and described from the Upper Eocene of Los Santos, Panama. The early ontogenetic development of the conch is shown by a median longitudinal section.

SCHUCHERT (1935, p. 590) recently quoted Olsson as stating that the nautiloids which occur in the Eocene of Los Santos, Panama, are referable to *Aturia*. These cephalopods had previously (MacDonald, 1919, p. 364) been referred to *Enclimatoceras* [=*Hercoglossa*]. Dr. Olsson kindly loaned us for study several specimens from Los Santos. All of these appear to be conspecific, and they are typical of the genus *Aturia*. As no Tertiary nautiloids have been illustrated or described from Central America proper and as the specimens under consideration are fairly complete and well preserved, it seems to us that a detailed study of them should be published.

Long ago Giraud (1903, p. 130) noted the occurrence of *Aturia* on Martinique in the Caribbean region, and more recently this genus has been recorded from Venezuela, Colombia, Ecuador, and Peru, as well as Chile and Argentina and the Chilean portion of Tierra del Fuego. Furthermore, representatives of it have been described from northern Mexico, both coasts of the United States, and Alaska. In the Eastern Hemisphere the genus is equally widespread. Stratigraphically it ranges from the Eocene up into the Pliocene.

Only one species of *Aturia*, *A. peruviana* Olsson, is known to be represented in the lower Tertiary of Venezuela, Colombia, and Peru, and the Panama specimens appear to be conspecific. The syntypes of *A. peruviana* came from the Saman or Talara formation (upper Eocene), the Mirador conglomerate member of the Mancora formation (middle Oligocene), and the Cone Hill shale member of the Heath formation (upper Oligocene) at several localities in northwestern Peru. Also, specimens that may be conspecific occur in the lower Oligocene Chira formation of northwestern Peru and in the uppermost Eocene near El Carmen in northern Colombia and near Santa Rita in northwestern Venezuela. Furthermore, it seems probable that the same species is represented by the Aturias which according to Sheppard (1937, pp. 55, 74) occur in the upper Eocene Socorro sandstone of southwestern Ecuador.

According to Olsson, the specimens under consideration came from the oldest paleontologically dated rocks in Panama, that is, from certain Eocene beds at Bucaru near the mouth of the Tonosi River in the province of Los Santos. These Eocene beds are fairly thick there and they consist largely of sandstone in which occur fossil zones crowded with *Venericardia* and *Aturia*. The sandstones have only a limited development and are not known outside of the Tonosi region. They are overlain apparently disconformably by late upper Eocene calcareous beds. Olsson correlates the sandstones at Bucaru with the early upper Eocene Talara formation of northwestern Peru, and the occurrence of *A. peruviana* in both of them is, to say the least, compatible with this correlation.

We wish to take advantage of this opportunity to acknowledge our indebtedness to Dr. A. A. Olsson of Gloversville, New York, who loaned us the specimens on which this study is based; to Mr. Howard Webster of Iowa City, Iowa, who retouched the photographs that accompany this report; and to Mr. Frederick O. Thompson of Des Moines, Iowa, who generously provided the funds that enabled us to complete this study for publication.

ATURIA PERUVIANA Olsson

Plate 13, figures 1, 2; plate 14, figure 2

Enclimatoceras sp. MACDONALD, *1919*, Am. As-

soc. Petroleum Geologists, Bull., vol. 3, p. 364.
Aturia alabamensis peruviana OLSSON, *1928*, Bull. Am. Paleontology, vol. 14, pp. 96–99, pl. 24, figs. 1–3.
(?) *Aturia colombiana* ANDERSON, *1928*, California Acad. Sci., Proc., 4th ser., vol. 17, pp. 17–18, text figs. 2, 3, pl. 1, fig. 10.
(?) *Aturia alabamensis peruviana?* SCHENCK, *1931*, California Univ., Dept. Geol. Sci., Bull., vol. 19, p. 546 (footnote 53).
Aturia sp. OLSSON, *1935*, in SCHUCHERT, Historical geology of the Antillean-Caribbean region . . . , p. 590.
Aturia peruviana MILLER and THOMPSON, *1937*, Eclogae geol. Helvetiae, vol. 30, pp. 64–68, text figs. 2A, 3, pl. 8, figs. 1–4; pl. 9, fig. 5.—MILLER and FURNISH, *1938*, Jour. Paleontology, vol. 12, pp. 152–153, text fig. 2.

Detailed descriptions of this species have been published by Olsson and by Miller and Thompson. Since these works are readily available to most paleontologists, it is not necessary for us to duplicate them. The Panama specimens we are studying are typical in all respects. The figured specimen, which is one of the largest of the nine we are studying, attains a maximum diameter (measured across the umbilicus) of about 110 mm and a maximum width and height of conch of about 63 mm and 65 mm, respectively. The specimens are preserved in glauconitic calcareous sandstone. For the most part they are internal molds, but considerable portions of the test adhere to some of them.

The inner volutions of these specimens are characteristically preserved in crystalline calcite, and of the three that we sectioned, only one retained details of the internal structures. A median longitudinal thin section of this specimen (see figure 2 on plate 2) shows the position and nature of the siphuncle during the various stages of growth. In the extreme adapical portion of the conch the siphuncle is subcentral in position, but in the first half of the first volution it migrates to a dorsal position, which it retains throughout the rest of its ontogenetic development. At its passage through the first septum the siphuncle is distinctly removed from the dorsal wall of the conch, but at the second septum it is in contact with that wall. In the sectioned specimen the septal necks and connecting rings are precisely similar to those of conspecific specimens from the Eocene of Venezuela, which we (1938, pp. 152–153, text figure 2) recently described in detail. In the adapical volutions of our specimen there is preserved a small subcylindrical tube in the center of the siphuncle. Its diameter is equal to about one-third the inner diameter of the siphuncle. Presumably this tube represents part of the siphuncular structure, which normally was not calcified. Spath (1933, p. 440) states that in each of the two examples of *Aturia aturi* that he sectioned "the first three septa were very thin and the fourth of abnormal thickness," but in our specimen there is a regular progressive increase in the thickness of the septa during early ontogenetic development.

Types.—The specimens on which this report is based are to be deposited in the Palaeontological Research Institution at Ithaca, New York.

Occurrence.—In Panama this species is so far known from only the lower part of the upper Eocene on the beach between the village of Bucaru near the mouth of the Tonosi River and Punta Guanico, in the province of Los Santos. Its occurrence in Peru, Colombia, Venezuela, and probably Ecuador is discussed above.

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JOURNAL OF PALEONTOLOGY, VOL. 13, NO. 1, PP. 79–81, PLS. 13, 14, 2 TEXT FIGS., JANUARY, 1939

AN ATURIA FROM THE NORTHWEST DIVISION OF WESTERN AUSTRALIA

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AND
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ABSTRACT—A well-preserved specimen, an internal mold, from near Merlinleigh Homestead, Western Australia, is illustrated and described as *Aturia* cf. *A. ziczac* (Sowerby). The age of the beds from which this specimen came is uncertain.

THE LITERATURE contains numerous references to the occurrence of *Aturia* in southern Australia (Victoria, South Australia, and Western Australia), as well as in Tasmania and New Zealand, but insofar as we have been able to ascertain no representative of this ubiquitous genus has been described from the northern portion of Australia. However, recently Condit, Raggatt, and Rudd (1936, p. 1059) mentioned that J. Thompson found an *Aturia* near Merlinleigh Homestead in the Northwest Division of Western Australia, far from any locality that had yielded congeneric forms and "about 90 miles inland from known Tertiary rock occurrences." In view of the fact that this specimen came from a remote region and is exceptionally well preserved, it seems to merit detailed study.

Condit, Raggatt, and Rudd (1936, p. 1059) believe it "quite possible" that the specimen under consideration was "derived from the disintegration almost *in situ* of a Tertiary (Eocene-Miocene) deposit," and it was hoped that a detailed study of this specimen would yield a more nearly precise age determination. It is difficult to make significant generalizations in regard to representatives of *Aturia*, for many of the described forms came from beds of uncertain age, and the published illustrations and descriptions of others are based on crushed and fragmentary specimens and are not accurate in detail. Newton (1919, p. 163) apparently was of the opinion that the Miocene *Aturias* have "a much more compressed shell and . . . a more elongate aperture" than do the congeneric Eocene forms. It seems to be true that the shells of the more primitive representatives of the genus, like the inner volutions of the more advanced ones, tend to be relatively broad, but compressed, subdiscoidal forms occur in the Eocene as well as in the Miocene. Likewise, Aturias with advanced types of sutures occur in both the Eocene and the Miocene. Nevertheless, insofar as we have been able to ascertain, primitive forms with relatively broad conchs and simple sutures, like the Western Australian specimen we are studying, are not known from the Miocene. Therefore the available evidence, which, to be sure, is very meager, would seem to indicate that the specimen under consideration is probably early Tertiary in age.

Numerous specific names have been proposed for various representatives of *Aturia*, but we are very uncertain as to just which

one to use for our specimen. McCoy (1876, p. 21) coined the name "*australis*" for some Aturias from the Tertiary of Victoria, and naturally there has been a tendency among paleontologists to apply that name to all congeneric forms found in Australia. However, Newton (1919, p. 164) was convinced that "*A. australis* presented no differences of importance from the true *A. aturi* of Europe, and therefore it should be known

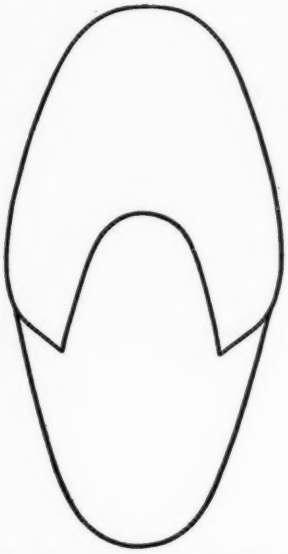


FIG. 1.—Outline ventral view (somewhat restored) of *Aturia* cf. *A. ziczac* (Sowerby) from near Merlinleigh Homestead, Western Australia, ×1.

under the latter name, a view which was fully confirmed in a verbal statement by the late Mr. G. C. Crick," but which is not shared by Chapman (1921, pp. 12–16). Anyhow, the type specimens of *A. australis*, like those of typical representatives of *A. aturi*, are more strongly compressed and therefore more nearly discoidal than the specimen under consideration, and our specimen seems to resemble much more closely *A. ziczac* (Sowerby), which was originally described from the London clay (Eocene) of England. However, fragments which adhere to the specimen we are studying show that originally the phragmacone consisted of at least one more full volution, and of course its characters may have changed somewhat in the outer portion of the shell. In view of these facts, and because of the uncertainty in regard to the age of our specimen, we have decided that for the present at least it will be best for us merely to term this specimen *Aturia* cf. *A. ziczac* (Sowerby).

We wish to acknowledge our indebtedness to Dr. W. M. Furnish, who prepared the drawings which accompany this report and offered valuable criticisms during the preparation of our manuscript; to Mr. Howard Webster, who retouched the photograph of the figured specimen; and to Mr. Frederick O. Thompson, of Des Moines, Iowa, who generously provided the funds which enabled us to complete this study for publication.

ATURIA cf. A. ZICZAC (Sowerby)

Plate 14, figure 1; 2 text figures

Aturia sp. CHAPMAN, *1936*, in CONDIT, RAGGATT, and RUDD, Am. Assoc. Petroleum Geologists, Bull., vol. 20, p. 1059.

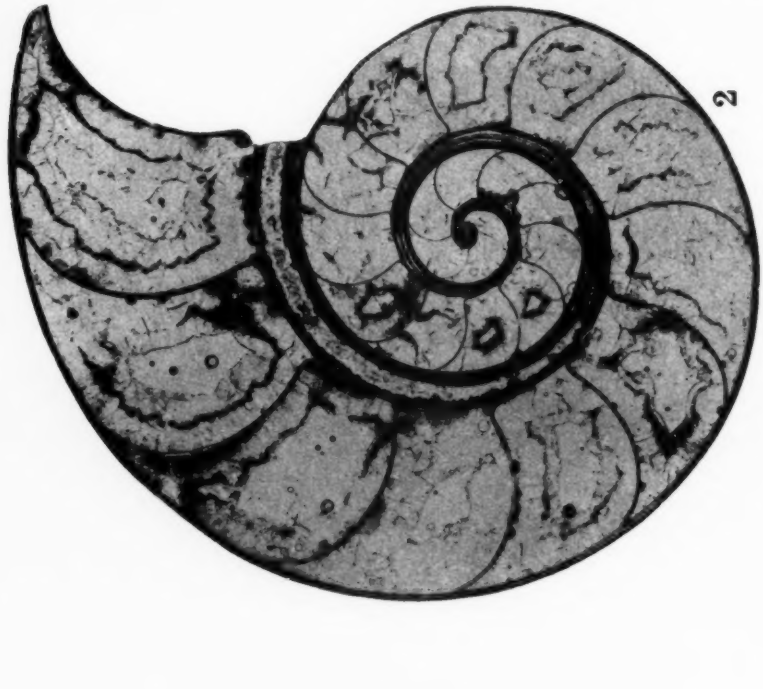
Conch nautiliconic, sublenticular, and moderately large—preserved part of phragmacone attains a maximum diameter (measured across the umbilicus) of about 73 mm, and fragments which adhere to this specimen show that originally the phragmacone consisted of at least one more full volution and attained a maximum diameter of more then 300 mm. Whorls compressed, flattened laterally (with lateral sides of conch converging ventrad), rounded ventrally, impressed dorsally, and about four-fifths as wide as high—impressed zone is about two-fifths as deep as conch is high. Length of living chamber and nature of growth-lines not known. Umbilicus closed and inconspicuous. Umbilical shoulders low, broadly rounded, and indefinite.

Septa rather closely spaced, and there are about eleven camerae to the volution. At maturity each suture forms a high, broad,

EXPLANATION OF PLATE 13

FIGS. *1, 2*—*Aturia peruviana* Olsson. Ventral and lateral views, ×1, of a typical specimen, an internal mold, from the upper Eocene at Bucaru near the mouth of the Tonosi River in the province of Los Santos, Panama. See also figure 2 on plate 14. (p. 77)

Miller and Furnish, *Aturia peruviana* from Panama



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1

Miller, Furnish, and Crespin, Tertiary Aturias

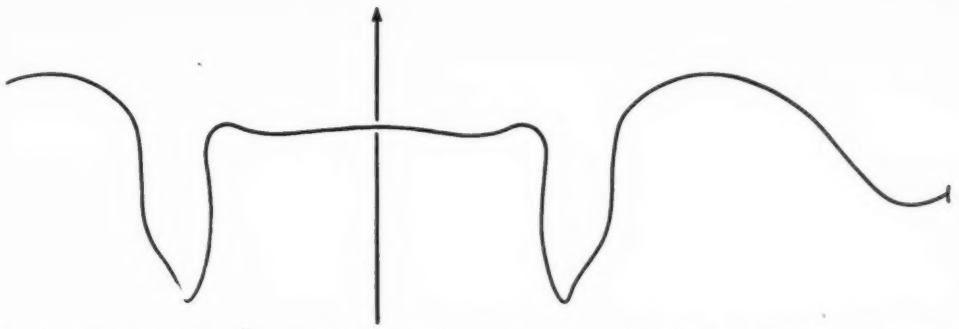

FIG. 2.—Diagrammatic representation of an external suture of *Aturia* cf. *A. ziczac* (Sowerby) from near Merlinleigh Homestead, Western Australia, ×1½.

almost flat more or less square-shouldered straight-sided ventral saddle and on either side of it a much narrower asymmetrical pointed tongue-shaped lateral lobe, a broad, high broadly rounded asymmetrical lateral saddle, a moderately deep rather narrowly rounded asymmetrical lobe on the umbilical portions of the conch, and a broad rather shallow broadly rounded asymmetrical internal lateral saddle, which extends to the dorsal lobe (see text figure 2). The shape of the dorsal lobe can not be ascertained from the specimen under consideration, but presumably it is deep, narrow, and spatulate. The top of the ventral saddle is slightly sinuous, and a pair of very shallow rounded secondary lobes, one on each side of the venter, divides it symmetrically into three low rounded secondary saddles. Siphuncle moderate in size and located close to the dorsum in an adapical infundibular flexure of the septa.

Remarks.—The specimen on which the above description is based is an internal mold preserved in dark-brown silicified ferruginous sandstone. Only one side of it is freed from the matrix, and it appears to have been very slightly distorted during preservation.

Occurrence.—Two miles northeast of Merlinleigh Woolshed, Northwest Division, Western Australia.

Figured specimen.—Commonwealth Paleontological Collection, Canberra, F. C. T., Australia.

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NOTE: Manuscript received by the Editor May 1, 1938.

EXPLANATION OF PLATE 14

FIG. *1*—*Aturia* cf. *A. ziczac* (Sowerby). Lateral view, ×1½, of a well-preserved internal mold from near Merlinleigh Homestead, Northwest Division, Western Australia. (p. 80)

2—*Aturia peruviana* Olsson. Median longitudinal section (unretouched photograph), ×3, of a typical specimen from the upper Eocene at Bucaru near the month of the Tonosi River in the province of Los Santos, Panama. See also figures 1 and 2 on plate 13. (p. 77)

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INADUNATE CRINOIDS OF THE MISSISSIPPIAN—ZEACRINUS

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ABSTRACT—The genus *Zeacrinus* is redefined and six new species from the Chester series are described. All species previously assigned to the genus are reconsidered on the basis of the revised description, and several have been deleted. All species that can, with some degree of certainty, be assigned to *Zeacrinus* are summarized in tabular form and listed in a bibliographic index. This revision restricts *Zeacrinus* to twenty-five Mississippian species.

TAXONOMY of Mississippian inadunate crinoids is badly in need of revision. Descriptions of new species have appeared more or less sporadically for many years. Only occasionally has there been a publication dealing with more than a few species of one or more genera. No attempt has been made to unify the results of the several workers since Wachsmuth and Springer (31) revised the Paleocrinoidea in the years from 1879 to 1886. This is the first of a contemplated series of papers by the senior author and graduate students in paleontology at the University of Illinois attempting to bring the synonymy to date, to epitomize all data pertaining to each genus, and to describe new species. This paper discusses only *Zeacrinus*. A paper treating *Eupachycrinus* and related forms is now in preparation.

In 1850 Dr. G. Troost (2, 31, 33) proposed in manuscript the name *Zeacrinites* for a crinoid specimen previously described as *Cyathocrinus magnoliaeformis*. The name was changed to *Zeacrinus* by Hall in 1858. Between 1850 and the preparation of this manuscript, fifty-seven species of *Zeacrinus* were described. This paper describes six new species, all Chester forms. Prior to 1926, thirty forms had been removed from the genus for various reasons and placed in other genera as follows: 16 species, *arboreus*, *asper*, *coxanus*, *elegans*, *merope*, *paternus*, *perangulatus*, *planobrachiatus*, *pocillum*, *ramosus*, *sacculus*, *sacculus* var. *concinnus*, *scobina*, *scoparius*, *serratus*, and *troostanus* in *Woodocrinus;* five species, *acanthophorus*, *armiger*, *depressus*, *discus*, and *mucrospinus* in *Hydreionocrinus;* five, *crassus*, *formosus*, *maniformis*, *mooresi*, and *subtumidus* in *Eupachycrinus;* two, *cariniferus* and *lyra* in *Coeliocrinus;* one, *stimpsoni* in *Decadocrinus;* and one, *pikensis* in *Pachylocrinus*.

From this quantitative analysis it would appear that the greatest difficulty has been experienced in the separation of species of *Woodocrinus* and *Zeacrinus*. However, Wachsmuth and Springer (31) assigned to *Woodocrinus* a large number of species which do not properly belong in that genus. That Springer later recognized this error is indicated by the following quotation from a publication of his (27, p. 77) in 1926:

> Much confusion in the literature was caused by the action of Wachsmuth and Springer in 1886, in referring to this genus (*Woodocrinus*) a large number of American species previously ranked under *Pachylocrinus*, *Zeacrinus*, etc. Subsequent consideration has shown that the arrangement was not well founded, and it should be disregarded.

At that time he restored *elegans* to *Zeacrinus*, reassigned *arboreus* and *scoparius* to *Pachylocrinus*, and transferred *florealis* from *Zeacrinus* to *Pachylocrinus*. We believe that *arboreus* is more properly assigned to some other genus, probably a new one, and that the same is true of *elegans*. Our study shows that none of the above remaining species should be retained in *Woodocrinus*. We are restoring *coxanus*, *merope*, *paternus*, *planobrachiatus*, *pocillum*, *ramosus*, and *troostanus* to *Zeacrinus*. The species *asper* and *scobina* are assigned tentatively to *Pachylocrinus*. All of the other species that were transferred from *Zeacrinus* to other genera were properly removed from *Zeacrinus*. Several of them probably should be assigned to new

genera. We are not attempting such assignment but are limiting our work to those species that we believe belong in *Zeacrinus*. Not all of the five placed in *Eupachycrinus* belong in that genus. Their disposition will be considered in a later paper.

We have accepted as the most reliable generic characters of *Zeacrinus* (1) a concave base, (2) extra primibrachs in the anterior ray, and (3) all brachials quadrangular except the axillaries; and have admitted no new species to the genus unless they conform in these requirements, although some of the older species, established on specimens incomplete in some respects, have been retained. Based on the above generic determinants there are several more species that should be removed from *Zeacrinus*. *Blairi* Miller and Gurley (21, p. 66) does not possess any extra primibrachs in the anterior ray. *Bursaeformis* White (27, p. 79 and 31, p. 351, 1879) although possessing only one primibrach in all the rays except the anterior, which has a greater number, possesses a turbinate base and so can not belong in *Zeacrinus*. Also some of the arm plates tend toward a wedge shape. It possibly belongs in *Poteriocrinus*. *Dubius* Miller and Gurley (17, p. 361) is placed in *Coeliocrinus*. *Girtyi* Springer (27, p. 84) differs from normal *Zeacrinus* in possessing an extra primibrach in each of the rays, and arms that branch differently from *Zeacrinus*. This is a Pennsylvanian form and may represent a new genus. *Bellulus* Miller and Gurley (18, p. 34) is probably a *Scytalocrinus*. *Cylindricus* Miller and Gurley (19, p. 38) and *nitidus* Miller and Gurley (18, p. 36) are assigned to Kirk's new genus *Phanocrinus* (5, p. 602). Kirk included in that genus forms like Z. *pulaskiensis* Miller and Gurley (20, p. 47), which we consider generically distinct from *Phanocrinus* as exemplified by the genotype, *Eupachycrinus formosus* Worthen. The relationship of forms like this will be considered in a future paper. *Durabilis* Miller and Gurley (20, p. 48) is placed in *Eupachycrinus*, while the disposition of *intermedius* Hall (3, p. 681) like *blairi* is in doubt. *Cylindricus*, *durabilis*, *intermedius*, and *nitidus* possess no extra primibrachs in the anterior ray. The arms of *pulaskiensis* extend above the radials without bifurcation, but in *durabilis* the posterior arm resting on the posterior sloping surface of the primibrach in each lateral ray does not bifurcate. For these reasons the species enumerated are deleted from *Zeacrinus*. This revision of *Zeacrinus* leaves in the genus 25 species, all of which are of Mississippian age.

Most of the work on *Zeacrinus* was done between the years 1850 and 1898. In the latter year Stuart Weller in his "Bibliographic Index of North American Carboniferous Invertebrates" climaxed that period of research. Very little has been done since. Only two or three articles have been published, the most important being that of Springer (27) in 1926, in which he tried to iron out some of the difficulties of classification with respect to the genus and stated several conclusions with which we do not agree. The points of disagreement will be discussed later.

We feel some hesitancy about assigning one of our new species, *lineatus*, to *Zeacrinus* because of the unusual character of the anal or posterior interray. However, in all other characters, so far as can be determined, it conforms to *Zeacrinus*. It seems hardly necessary, therefore, to erect a new genus to care for it.

New species of *Zeacrinus* are described from specimens collected in Illinois and Kentucky and obtained from Walker Museum, the University of Chicago. Specific types loaned by Walker Museum have been of great aid in identification and determination of new species. The authors acknowledge the kindness of this institution for the loan of their material. It has not been possible to procure for study all types of described species, although this has been done in as many instances as possible. In addition to specific descriptions, this paper contains a revised description of *Zeacrinus* and a bibliographic index of all other accepted species of the genus.

DIAGNOSIS OF THE GENUS

Class CRINOIDEA Miller

Order INADUNATA Wachsmuth and Springer

Suborder FISTULATA Wachsmuth and Springer

Family POTERIOCRINIDAE Roemer
(emend. Wachsmuth and Springer)

Genus ZEACRINUS (Troost) Hall, 1858

Genotype, *Cyathocrinus magnoliaeformis* Owen and Norwood.

Zeacrinites TROOST, *1850*, Proc. Am. Assoc. Adv. Sci., vol. 2 (read 1849), p. 61 (nomen nudum); MSS.

Zeacrinus HALL, *1858*, Iowa Geol. Survey Rep., vol. 1, pt. 2, p. 544.—MEEK and WORTHEN, *1860*, Geol. Rep. III, vol. 2, p. 186.—SHUMARD, *1866*, Acad. Sci. St. Louis, Trans., vol. 2, no. 2, p. 398.—WACHSMUTH and SPRINGER, *1879*, Acad. Nat. Sci. Philadelphia, Proc., pp. 348–352.—MILLER, *1899*, North American Geol. and Pal., p. 288.—WOOD, *1909*, U. S. Nat. Museum, Bull. 64, p. 89.—BATHER, *1900*, A Treatise on Zoology, vol. 3, The Echinoderma, p. 180; *1911*, Edinb. Geol. Soc., vol. 10, p. 61.—ZITTEL, *1913*, Textbook of Paleontology, vol. 1, p. 223.—WRIGHT, *1917–1918*, Geol. Soc. Glasgow, Trans., vol. 16, pt. 3, p. 380.—SPRINGER, *1926*, U. S. Nat. Mus., Proc., vol. 67, art. 9, pp. 77–85.

Dorsal cup low, shallow, bowl-shaped, broader than high. Tegmen vaulted or conical, four or five times as high as the dorsal cup. Arms heterotomous, uniserial, and pinnulate. Column circular, perforated by a small axial canal, and deeply impressed in the base of the dorsal cup. Dicyclic. Infrabasals five, usually hidden in the cavity of the dorsal cup by the column. Basals five, occasionally visible in a lateral view of the dorsal cup but more often visible only from below. They bend upward into the basal cavity, are pentagonal, hexagonal, or heptagonal; the greatest variation in form occurring in the basal adjacent to and left of the anal interray. Radials five, pentagonal, convex outward, angular below, truncated above; greatest width along the upper surface; generally wider than high although in some species they are more elongated and project farther into the basal cavity. All brachials quadrangular except the axillaries. Each ray contains one cuneiform axillary primibrach, which rests on the truncated surface of a radial except in the anterior ray, where it always surmounts one, two, or as many as five additional quadrangular primibrachs. The axillary primibrachs are usually broader than high, the superior, slightly concave sloping edges, each of which supports an arm, may be equal or subequal in width. The number of secundibrachs in each arm varies from three to 11. Above the cuneiform axillary secundibrachs, which lie above the rectangular secundibrachs, the arms bifurcate again. The middle two of the four branches thus produced on each ray are narrower than the outer two, and usually extend upward without further bifurcation, often becoming narrower in the distal portion. The two outer arms continue to divide at intervals into rami of nearly equal width.

There are no interradial plates except in the anal interray, which consists of four or more plates of various shapes, sizes and arrangements. The posterior or anal interray has been the subject of much discussion and differences in nomenclature. The two lowest plates are uniformly designated radianal and anal *x*. For the additional plates diverse nomenclature has been used. Some writers speak of them as anal plates and others as tube plates. We are designating all plates of the posterior interray, which possess flattened exteriors and extend out approximately as far as the brachials, as radianal, anal *x*, and 2nd, 3rd anal, etc. We recognize that the plates of the anal or posterior interray bore no close relation to the anus, which was situated in different positions in different species, at almost any position in the ventral sac from top to bottom, and even on the anterior side. The plates of the posterior interray evidently helped to support the ventral sac. In most forms they were situated on and outside of other plates of the sac. This is especially noticeable in those forms that possessed a five-sided pyramidal sac. (See plate 1, fig. 14.) The acute ridges in four interradial positions are composed of only one series of plates, whereas in the posterior interray there are two. The plates that we are designating anal plates may be identified by the flat exterior surface. The externally visible portion of the series ends with a flat-surfaced top plate, which has an acute distal angle, although two series of plates in the posterior interradial position continue nearly to the top of the ventral sac.

The characters of the ventral sac and position of the anus vary in the different species of *Zeacrinus*. Typically, the ventral sac is a five-sided pyramid. Springer (27, pp. 64–69) has given a good discussion of

these features of inadunate crinoids. The number of anal plates incorporated in the dorsal cup varies. The radianal is always below the radial-primibrach suture. In most forms anal *x* is partly in the cup and usually anal 2 is partly below the radial-brachial suture. Above the top of the radials the remaining anal plates continue in about the same surface as the brachials.

Springer has diagrammed the anal interrays of several specimens (27, p. 83, figs. 1–9). It should be noted that he had grouped under the same species specimens which have anal interrays that are notably different. According to the basis of classification herein advocated, these would be placed in different species. He says (27, p. 78) that

> Variations in the structure of the anal side have caused some confusion in an attempt to formulate a generic diagnosis which would reconcile the differences between the earlier and later species. In the typical Chester species, *Z. wortheni*, the radianal is a long and narrow plate, often passing down between two basals almost to a contact with the infrabasals—a form and position so unusual that it has attracted special attention. But all species from the earlier formations are now known to have a short and broad radianal; and it appears that in the very latest species of all, from the Pennsylvanian, the earlier form of radianal was resumed. Therefore such a range of variation in character must be accepted for the genus.

This fact, in the opinion of the writers, does not invalidate the anal interray as a reliable specific determinant since many groups of organisms in racial old age display characters more like those of earlier forms than those of their immediate ancestors. It should also be noted that we recognize no Pennsylvanian species of *Zeacrinus*, so that the reference to a short and broad radianal for Pennsylvanian forms is not pertinent. However, some of the Chester species possess a rather short and broad radianal.

This variation in character of the anal side is accepted by us for the genus, but we do not recognize such a variation within a given species as Springer does (27, pp. 81–83), for example in *Z. magnoliaeformis* or *Z. wortheni*.

Springer (27, p. 78) believed concerning the genus,

> that the only stable character is the heterotomous arm branching, with mostly uniserial, short, and distally quadrangular brachials. Within this may occur depressed or narrow anal area; long or short radianal; flat or rounded arms; club or balloon-shaped or pyramidal sac; round or pentagonal stem,

and on this basis he established several species which may more properly be classified elsewhere. It is the opinion of the authors that the arm branching may be stable in that it is heterotomous, but that its constancy as to the number of branches formed is not great enough to make it a reliable specific determinant, as Springer believed.

It is a generally accepted principle that the character of those plates which lie within the calyx and nearer to the body is more stable than that of the arms. The determination of species has been based on certain consistent characteristics which we consider more stable, namely: shape, arrangement, size, and number of plates in the anal interray and the number of extra primibrachs in the anterior ray. It seems probable that the variations in number and position of the secundibrachs in each arm, as well as the number of bifurcations in each ray are not constant enough to warrant their use as specific determinants. They are better interpreted as individual variations.

Another generic character, which seems to be stable, is the presence of extra primibrachs in the anterior ray and their absence in the other four. Springer included a few exceptions to this general rule. We have not admitted to the genus any new species that have extra primibrachs in any of the rays other than the anterior; in fact, we have removed the species *dubius* (17, p. 361) and *girtyi* (27, p. 84) from the genus because of extra primibrachs in these four rays.

Springer (27, p. 79) considered that, "*Zeacrinus* ranges through the entire Lower Carboniferous, beginning in the Kinderhook, culminating in the Chester, and passing up into the Pennsylvanian." Our interpretation recognizes no species of *Zeacrinus* younger than Mississippian.

Some species that have been described—*bifurcatus* McChesney (9, p. 7), *compactilis* Worthen (13, p. 536), *keokuk* Worthen (35, p. 303 and 34, p. 28), *magnoliaeformis* (Troost) (3, pp. 544, 684 and 36, p. 90), —*salemensis* Miller and Gurley (19, p. 37), and *spinuliferis* (Worthen) (35, p. 90)—were

based on specimens incomplete either in the anal interray or the anterior ray. This has made comparison of species and identification of specimens very difficult. In this paper no species are described if the specimens are not complete in both of the specific determinants. At the beginning of the description of each species are two numbers, the first of which indicates the number of plates in the anal interray, and the second the number of extra primibrachs in the anterior ray. These data are assembled in the table, which includes all species that have been described and which can, with some degree of certainty, be assigned to *Zeacrinus*.

Since this manuscript was prepared an important paper treating *Zeacrinus* has been published by Edwin Kirk (5*a*). This paper is of special significance because in it Kirk assigned species which we deleted from *Zeacrinus* to new genera, thus agreeing with several of our conclusions. Points of agreement and disagreement are briefly considered in this additional note.

Zeacrinus girtyi Springer, which we removed from the genus and considered probably a new genus, he made the type of a new genus, *Alcimocrinus* (p. 162). *Zeacrinus bursaeformis* White, which we tentatively assigned to *Poteriocrinus* has been made the type of a new genus, *Cercidocrinus* Kirk (p. 163). In the same genus he also placed *Zeacrinus blairi* Miller and Gurley, which we deleted from *Zeacrinus* without reassigning it; *Zeacrinus infrequens* Laudon and Beane, and three other species previously assigned to other genera.

Zeacrinus nodosus Wachsmuth and Springer and *Zeacrinus compactilis* Worthen are considered as the two species of another new genus, *Adinocrinus*, of which *nodosus* is the genotype. *Zeacrinus arboreus* Worthen, which we considered as probably representing a new genus, together with several other forms previously assigned to *Zeacrinus*, Kirk placed in a new genus, *Linocrinus* (p. 168). Among the species of *Linocrinus* he included *Zeacrinus scobina* Meek and Worthen and *Z. asper* Meek and Worthen, which we tentatively placed in *Pachylocrinus*.

Our major disagreement with Kirk's classification is in the assignment of certain

SPECIES OF ZEACRINUS

Name	Number of plates in anal interray	No. of extra primibrachs in anterior ray	Age
acuminatus Sutton and Hagan	8	1	Golconda
bifurcatus McChesney	3 visible	2	Chester
brevilatus Sutton and Hagan	7	2	Glen Dean
chesterensis Sutton and Wagner	5	2	Paint Creek
coxanus Worthen	?	1	Keokuk
doverensis Miller and Gurley	7	2	Chester
fusiformis Sutton and Hagan	7	2	Renault
grandiculus Miller and Gurley	9	1	Chester
kentuckiensis Miller and Gurley	7	1	Chester
keokuk Worthen	?	3	Keokuk
lanceolatus Sutton and Hagan	6	1	Paint Creek
lineatus Sutton and Hagan	5	1	Glen Dean
magnoliaeformis (Owen and Norwood)	?	1	Chester
merope Hall	?	2	Waverly
obesus Miller and Gurley	4	2	Chester
ovalis Lyon and Casseday	8	1	Chester
paternus Hall	?	5	Waverly
peculiaris Miller and Gurley	5	1	Glen Dean
planobrachiatus Meek and Worthen	3 visible	?	Keokuk
ramosus Hall	4 visible	4	Burlington
salemensis Miller and Gurley	5 visible	?	Keokuk
spinuliferus (Worthen)	5 visible	3	Chester
trapeziatus Sutton and Hagan	7	1	Chester
troostanus Meek and Worthen	3 visible	3	Burlington
wortheni Hall	5	2	Chester

species to the new genus *Eratocrinus* (p. 165). *Zeacrinus elegans* Hall, which we considered as probably belonging in an unnamed genus, was selected as the genotype. Among others he included *Z. coxanus* Worthen, *Z. ramosus* Hall, *Z. salemensis* Miller and Gurley, and *Z. troostanus* Meek and Worthen, species, which after a study of most of the types, we have retained in *Zeacrinus*.

NEW SPECIES

ZEACRINUS LANCEOLATUS Sutton and Hagan, n. sp.

Plate 15, figures 11–13; text figure 2

6–1.[1] Dorsal cup low, circular in outline. Column circular, consisting of thin plates perforated by a small axial canal. Infrabasals hidden in the basal cavity. Basals five, tops of four angular, basal adjacent to and left of the radianal, somewhat narrower and truncated along the upper left side. Radials five, pentagonal, about two-thirds as high as wide, truncated on the upper edge along a concave suture line. The axillary primibrachs which rest on the radials in four of the rays have about the same height and width as the radials. The axillary primibrach in the anterior ray is shorter than those in the other rays and is separated from the radial by a quadrangular primibrach, which is twice as wide as high. There are four secundibrachs above each of the lateral sloping edges of the axillary primibrachs except the posterior edge of the one in the right anterolateral ray, which is succeeded by only three. The rami continue upward with further bifurcations until they total 38. The manner of division above the secundibrachs is as follows: the middle two of the four branches produced by the first division continue upward without further bifurcation except the posterior middle branch of the right posterolateral ray, which divides once. Each outer branch formed by the first division bifurcates and the outer branches formed by this second division divide once more, except the anterior outer branch of the right posterolateral ray and the outer branches of the anterior ray. The number of arms is six in the anterior ray and eight in each of the other four.

Anal interray (text fig. 2) composed of six plates, the radianal, anal *x*, and four additional plates. Radianal pentagonal, elongate, extending well into the basal cavity, wider at the top than bottom, entirely within the dorsal cup. It is truncated below on the right by a basal, on the right lateral edge by the radial, above by the first and second anals, and on the left by a basal. Anal *x* (first anal) pentagonal, slightly longer than wide, truncated on the left by the radial and primibrach, with its superior suture even with that of the top of the primibrach, above by the third anal plate, and on the right by the second anal and radianal. The second anal, which is hexagonal and about one-third longer than the first, lies above the radianal, to the right of the first and third anals, below the fourth, and to the left of the radial, primibrach, and the lower portion of the first secundibrach. It, like anal *x*, lies partially within the dorsal cup. Third anal pentagonal, smaller than the first and second anals, truncated on the left by the first secundibrach and the lower two-thirds of the second secundibrach, above by the fourth anal and on the right by the second anal. The large fourth anal is five-sided. All edges except the lateral are curved. Its upper edge is even with that of the third secundibrach on the left and the middle of the second secundibrach on the right. The triangular, apical fifth anal plate has an acute distal angle and truncates the fourth anal below, extends to the left superior edge of the axillary secundibrach on the right and to the top of the first tertibrach on the left. Character of the ventral sac unknown.

Remarks.—This species is very similar to *Zeacrinus kentuckiensis* Miller and Gurley in general appearance, but the chief specific difference lies in the anal interray, where the fourth anal plate differs in shape, the one in *Z. kentuckiensis* being pentagonal whereas the plate in this specimen is hexagonal and of greater width, the largest plate in the anal area. The apical plate is the largest in the anal interray of *Zeacrinus kentuckiensis*.

Horizon and locality.—The holotype of this species was collected in 1911 by Stuart

[1] This key combination refers to the number of plates in the anal interray and the number of extra primibrachs in the anterior ray.

Weller from the Paint Creek shale 1¼ miles northwest of Floraville, Illinois. It is number 26919 of the paleontological collection of Walker Museum at the University of Chicago.

width along the distal edges. The proximal angles are obtuse and the lower lateral sides are concave where the basals fit into them. Five primibrachs rest on the radials, four are pentagonal, cuneiform, and axillary, the

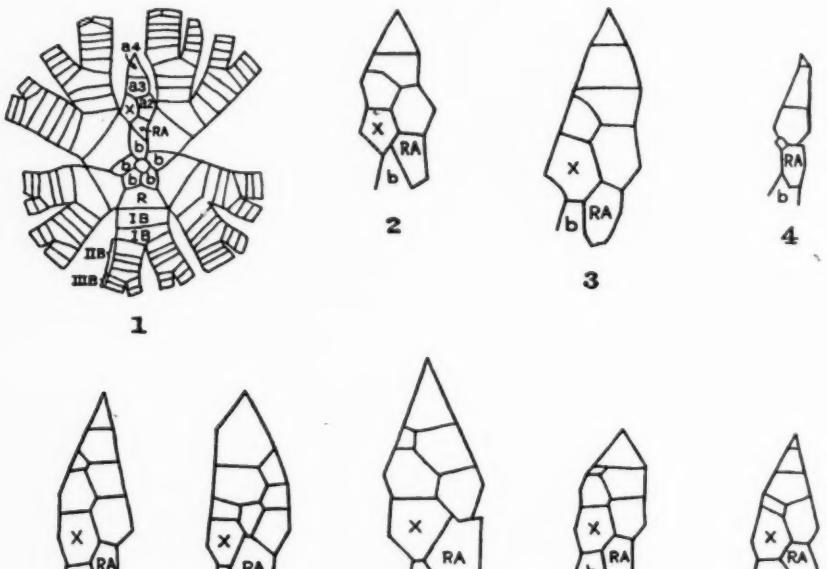

FIG. *1*—Analysis of the plates of the calyx of *Zeacrinus*, based on the holotype of *Z. peculiaris* Miller and Gurley. *b*, Basals; *R*, radials; *x* and *a*, anals; *RA*, radianal; *IB*, primibrachs; *IIB*, secundibrachs; *IIIB*, tertibrachs; infrabasals hidden by the column.
2–9—Analyses of the plates of the anal interray of species of *Zeacrinus*, ×2. *2*, *Z. lanceolatus* Sutton and Hagan. *3*, *Z. trapeziatus* Sutton and Hagan, n. sp. *4*, *Z. lineatus* Sutton and Hagan, n. sp. *5*, *Z. acuminatus* Sutton and Hagan, n. sp. *6*, *Z. grandiculus* Miller and Gurley. *7*, *Z. fusiformis* Sutton and Hagan. *8*, *Z. brevilatus* Sutton and Hagan. *9*, *Z. doverensis* Miller and Gurley.

ZEACRINUS TRAPEZIATUS Sutton and Hagan, n. sp.

Plate 15, figures 15–17; text figure 3

Calyx 1.7-1. Low, subrounded dorsal cup. Column large, round, filling the basal cavity and perforated by a small axial canal. Infrabasals hidden by the column. Basals five, four of which are angular distally and have distinctly convex superior edges, the fifth, which lies to the left of and adjacent to the radianal, is truncated above by anal *x*. The five pentagonal radials are approximately twice as wide as long with the greatest

fifth, in the anterior ray, is quadrangular and 3½ times as wide as high. Its superior truncated edge is surmounted by an axillary cuneiform primibrach similar to the other four. From four to seven secundibrachs rest upon each superior sloping edge of the axillary primibrachs, above these the arms continue upward, dividing irregularly except in the anterior ray where there is only one division in each ramus. The arms taper toward the periphery where they number 28.

The anal interray (text fig. 3) contains seven plates, six anals and one radianal.

The hexagonal radianal is long and narrow, with its greatest breadth at a point opposite the top of the basal on the left, and extends deep into the basal cavity. It is bounded on the right by a basal and a radial, the second anal truncates it, anal *x* lies adjacent to its left superior sloping edge and the truncated basal below. The radianal is the longest plate in the anal interray and lies entirely within the dorsal cup. The first and second anals are both noticeably elongate, twice as long as wide, and the lower portions of both lie in the dorsal cup. The heptagonal anal *x* truncates a basal below, the radianal with its lower right lateral face, the second anal with its upper right lateral face, and the third anal above. Its two left lateral edges extend from the top of the lower right lateral edge of the radial to the top edge of the primibrach. The hexagonal second anal rests on the radianal, lies adjacent to the radial, primibrach, and most of the first secundibrach on the right. Its superior edge is surmounted by the fourth anal, and its two lateral edges are adjoined by the third and first anal plates. The third anal was probably four-sided, somewhat shorter than the first two plates, and almost as wide as long, with the greatest width at a point opposite the upper facet of the second anal. From this point the plate narrows toward the distal edge. It lies between the second and fourth anals on the right, probably below the fourth anal, its extent on the left is perhaps to the top of the second secundibrach, and it truncates the first anal plate. The fourth anal is probably four-sided. Its greatest breadth is along the distal margin, which extends entirely across the anal interray beneath the fifth anal. The proximal edge rests on the second anal plate, the concave left side adjoins the third anal, and the right facet extends to the middle of the third secundibrach. The largest plate in the anal area is the trapezoidal fifth anal, whose base, the greatest width of the plate, truncates the fourth anal. On the right it extends to the top of the left superior sloping edge of the cuneiform axillary secundibrach. The relationship on the left is obscure. The sixth anal forms an equilateral triangular cap for this long slender anal interray.

Remarks.—The only other described species with the key combination, 7-1, is *Z. kentuckiensis*, which differs notably from *trapeziatus* in the arrangement of the plates in the azygous area.

Horizon and locality.—The holotype was collected from the Chester series in Monroe County, Illinois. It is number 9402 of the Gurley Collection, Walker Museum.

ZEACRINUS LINEATUS Sutton and Hagan, n. sp.

Plate 15, figures 7–8; text figure 4

5-1. Crown medium size. Dorsal cup low, saucer-shaped. Basal cavity deep. A small circular column partially fills the basal cavity, completely hiding the infrabasals.

A five-pointed starlike pattern is formed by the five distally acute basals, which lie almost entirely within the basal cavity. The right lateral upper edge of the basal to the left of the radianal is notched where the radianal fits into it. Radials five, pentagonal, about three-fourths as high as wide, angular below, truncated above for the support of the five primary brachials, four of which are pentagonal, cuneiform, and axillary; the fifth, in the anterior ray, is quadrangular and about three times as wide as long. This plate supports a short cuneiform axillary primibrach. Each superior edge of the axillary primibrachs bears a row of four secundibrachs, except the right superior edge of the primibrach in the left anterolateral ray, which supports only three.

The fusiform anal area (text fig. 4) is very narrow and extends barely to the edge of the basal cavity. It is one plate wide for the greater part of its length, with the exception of the place where a very minute anal *x* lies adjacent to the second anal. The area consists of five plates, three of them large and elongate, and two very minute. Radianal hexagonal, elongate, entirely within the dorsal cup, tapering from distal to proximal edge. Its left inferior edge and proximal edge abut a basal below; the right lateral edge is adjacent to the radial and extends as high as its superior truncated edge; distal edge truncated by the second anal plate; left superior lateral edge truncated by a very small quadrangular first anal plate, and left lateral edge truncated by the lower right lateral face of the radial in the left posterior ray. Anal *x* quadrangular, small, about one-twentieth the size of

the radianal, and partly within the dorsal cup. Its lower right edge truncates the upper left corner of the radianal, its upper right edge is adjacent to the second anal plate, the left superior face is truncated by the base of the primibrach to the left, and the lower left face is truncated by the right lateral edge of the radial. Second anal heptagonal, widest plate in the anal interray, greatest width one-third the distance above the proximal face, longer than wide. It truncates the radianal and anal *x* below, extends to the distal edge of the first secundibrach on the right, is truncated above by the third anal, and extends seven-eighths of the distance to the top of the first secundibrach on the left. Third anal trapezoidal, elongate, greatest width at base, tapers upward, rests on the second anal, lies below the minute fourth anal, and extends to the top of the third secundibrach on either side. The small apical plate of the anal interray is apparently triangular, its proximal edge rests on the truncated surface of the third anal, it extends to the superior edges of the axillary secundibrachs on either side, and is about one-third as long as the third anal plate.

Remarks.—This species is very distinct because of the shape and width of its narrow anal interray. *Zeacrinus peculiaris* Miller and Gurley (text fig. 1) closely approaches this species but differs from it in that anal *x* is larger and hexagonal. The second anal plate of *Z. peculiaris* is smaller than the first, hexagonal, and located on the right side of the anal interray as contrasted with a large heptagonal second anal, which extends entirely across the anal interray in *Z. lineatus*. The third anal differs noticeably in shape.

Another species, *Zeacrinus magnoliaeformis* Troost, has the one extra primibrach in the anterior ray as does *Z. lineatus*, but the number of plates in the anal interray of the former is unknown. Thus it is impossible to compare them.

Horizon and locality.—The holotype of this species was collected from the Glen Dean formation, Pulaski County, Kentucky, and is number 19125 in the Gurley collection of Walker Museum.

ZEACRINUS ACUMINATUS Sutton and Hagan, n. sp.

Plate 1, figures 4–6; text figure 5

8-1. The dorsal cup of the medium-sized crown is low. The small column which partially fills the basal cavity consists of circular plates, alternating in size, which are serrated on the outer one-half of their proximal and distal faces, and meshed much like cog wheels.

Infrabasals hidden by the axial column. Basals five, bent abruptly upward, almost at right angles, into the basal cavity, whose steep-sided walls they practically form. Superior lateral edges convex, distal portion angular in all except the truncated basal adjacent to and left of the radianal. Radials five, pentagonal, approaching close to the abrupt edge of the basal cavity, the one in the anterolateral ray barely entering it, the greatest width is about twice the height. In the anterior ray a quadrangular plate whose breadth is three times the height rests upon the radial and beneath a pentagonal axillary primibrach. The number of secundibrachs in the branches which rest on the sloping edges of the axillary primibrachs are three, four, or six. The uniserial arms continue upward with further unequal dichotomizing. The upper portion of the vaulted tegmen is well preserved and clearly visible.

Anal interray (fig. 5) of eight plates, one radianal and seven anals. Radianal elongate, pentagonal, entirely within the dorsal cup, truncated on the inferior edges by basals, on right lateral edge by a radial, above by the second anal, on the left superior lateral edge by anal *x*. Its proximal edge extends to the rim of the basal cavity but does not enter it. Anal *x* hexagonal, longer than wide, extends slightly above the top of the right sloping edge of the axillary primibrach on the left, lies below the third anal, to the left of the second anal and the radianal. Second anal hexagonal, extends on the right to the top of the first secundibrach, lies below the fourth anal, is truncated on the upper left corner by the third anal, adjoins the first anal on the left and rests on the radianal. The first and second anals lie partly in the dorsal cup. Third anal pentagonal, longer than wide, greatest width in the lower one-third, extends slightly above

the second secundibrach on the left, truncated above by the fifth anal, below by the first and on the right by the second and fourth anals. Fourth anal pentagonal, adjacent to the fifth and third plates on the left, the third plate extending four-fifths of the distance to the top, rests on the second anal, and extends to the middle of the third secundibrach on the right. The fifth anal is a small quadrangular plate, which is the smallest plate in the interray. It is hemmed in by the third anal below, the fourth anal on the right, the sixth anal above, and the axillary secundibrach on the left. Sixth anal pentagonal, rests on fifth and fourth anals, extends from the middle of the third secundibrach, along the fourth and the lower one-third of the fifth secundibrach on the right, lies below the seventh anal, and extends to the top of the first tertibrach on the left. An elongate trapezoidal plate with the greatest width at its base rests on the large sixth anal. This seventh anal extends to the middle of the third tertibrach on the left and slightly above the edge of the axillary secundibrach on the right. Another plate is visible above the seventh plate in the anal interray. This plate has an acute outer edge and lies below the general level of the other visible plates of the interray. The series of plates undoubtedly continues on into the structure of the ventral sac.

Horizon and locality.—The holotype was collected from the Golconda limestone 2½ miles northeast of Gowansville, Illinois, by Stuart Weller in 1917. It is number 26847 of the paleontological collection in Walker Museum.

ZEACRINUS FUSIFORMIS Sutton and Hagan, n. sp.

Plate 15, figures 9–10; text figure 7

7-2. Crown large. Dorsal cup low. Basal cavity almost completely filled by a circular column, which hides the infrabasals and the lower part of the basals.

Basals five, angular above, bases hidden, a trifle longer than wide. Basal to the left of radianal has its distal angle barely clipped by the narrow base of the first anal plate. Radials five, pentagonal, twice as wide as high, superior edges slightly concave. Primibrachs, which truncate radials, are axillary, pentagonal, and cuneiform in four of the rays. In the fifth or anterior ray the radial is truncated by a quadrangular primibrach twice as wide as high, upon which rests another quadrangular primibrach seven times as wide as high, which is surmounted by an axillary primibrach similar to those in the other rays but much shorter. Three to seven secundibrachs, in each of the ten arms, rest on the axillary primibrachs. They are quadrangular, except the cuneiform, axillary secundibrachs, and four times as wide as long. Arms extend upward, close together, almost parallel, and taper slightly. Each ray bifurcates into two arms of unequal width immediately above the secundibrachs, except the anterior ray, where the two arms are equal. The outside arms of the four thus formed in each of the other rays continue upward with one more unequal bifurcation; the inner arms continue without further division, producing six rami in the outer extremities of each ray. In the anterior ray the two arms bifurcate equally once, forming four rami. These divisions produce 28 uniserial arms in the outer periphery.

The anal interray (text fig. 7) is spindle-shaped, 2½ times as long as wide, acuminate above, and does not extend into the basal cavity. It contains seven plates, one radianal and six anals. Radianal pentagonal, truncated on the right by a radial, at its base by a basal, and above by the heptagonal first and hexagonal second anal plates. It lies entirely within the dorsal cup, is broader than long, with the greatest width near the distal faces. Anal *x* heptagonal, adjacent to the radial, primibrach, and one-half of the first secundibrach on the left; below third anal, and to left of second anal. It is slightly longer than wide, with its lower half in the dorsal cup. Second anal hexagonal, adjoined below by the radianal, by the first and third anals on the left, by the fourth anal above, and by the primibrach and two-thirds of the first secundibrach on the right. It lies partly within the dorsal cup, is slightly wider than long, with the greatest width approximately two-thirds of the distance above its base. Third anal pentagonal, between the second and fourth anals on the right, below the very small quadrangular fifth anal, and extending from the top one-third of the first secundibrach to the middle of the fourth secundibrach on

the left. Its greatest width is less than one-third the distance above its proximal side. The largest anal plate is the pentagonal fourth anal, which lies between the third and fifth anals, below the sixth, above the second, and extends from the top of the first secundibrach on the right to the middle of the axillary fourth secundibrach. The fifth anal plate is distinct because of its small size, about one-eighth of the fourth anal. It is quadrangular, lies above the third anal, below the sixth, to the left of the fourth anal, and to the right of the fourth and fifth axillary secundibrachs of the left posterolateral ray. The apical, acuminate, four-sided sixth anal plate tapers out between the arms, which close in above it from either side, truncates the fourth and fifth anals below, and extends on the right from the first axillary secundibrach to the fourth tertibrach and on the left from the base of the first tertibrach to the middle of the fifth.

Remarks.—This species (text fig. 7) has the same number of anal plates and extra primibrachs in the anterior ray as *Zeacrinus doverensis* Miller and Gurley (text fig. 9) and *Zeacrinus brevilatus* Sutton and Hagan (text fig. 8). It is distinct from both of these species. The distinctions will be pointed out in the description of the latter species.

Horizon and locality.—The holotype of this species was collected in 1911 by Stuart Weller from the Renault limestone 5½ miles southeast of Waterloo, Illinois, in the NW ¼ sec. 11, T. 35, R. 9 W. It is number 25579 of the paleontological collection of Walker Museum.

ZEACRINUS BREVILATUS Sutton and Hagan, n. sp.

Plate 15, figures 1–3; text figure 8

7-2. The low dorsal cup is somewhat semioval in shape as viewed from below. The small circular column, perforated by a minute axillary canal, hides the infrabasals in the deep basal cavity.

There are five basals, twice as long as wide, four of which have somewhat rounded distal angles and distinctly convex superior lateral edges, the fifth, which has very straight sides, is adjacent to and left of the radianal and is truncated above by anal *x*. The proximal edges are hidden in the basal cavity. Radials, five, pentagonal, one-third wider than high, wedge shaped below, proximal edges adjacent to basals concave, and curved well up into the basal cavity. Axillary, pentagonal, cuneiform primibrachs rest on the upper facets of all the radials except in the anterior ray, where two quadrangular primibrachs are inserted between the radial and the axillary primibrach. These two plates are equal in width, the lower being 2½ times as wide as high and the upper five times as wide as high. The number of secundibrachs in each ramus borne on the superior edges of the primibrachs is either four or six. The arms number 28 in the outer periphery, four in the anterior ray and six in each of the others. The distal ends of the outer arms are missing, and in some of these incomplete outer arms there are indications of further division. It may be that the outer periphery contained more than 28, possibly as many as 36 branches.

The anal interray (text fig. 8) contains seven plates, six anals and one radianal. The narrow, elongate, pentagonal radianal extends farther into the deep basal cavity than the radials. It is truncated below and on two-thirds of the left side by a basal, on the right by a radial, above by the second anal, and on the upper left by anal *x*. The hexagonal first anal, which is a trifle higher than wide and whose distal facet is only a fraction lower than a similar face on the second anal, is truncated by a basal below, by the radianal on the lower right lateral edge, by the second anal plate on the upper right lateral edge, by the third anal above, and by a primibrach on the upper left lateral edge. More than half of it lies in the dorsal cup, as does the second anal and all of the radianal. Its lower left and right lateral edges are concave. The second anal plate is approximately the same size as the first, hexagonal, truncated above, two lateral edges nearly parallel, and wedge-shaped below. It is truncated below by the radianal, on the lower right by a radial, on the right lateral face by the primibrach and first secundibrach, above by the fourth anal, on the upper left by the third anal, and on the left by anal *x*. Third anal smaller than first and second anals, hexagonal, greatest width near the base, rests on anal *x*, abuts second anal on lower right, adjacent to fourth anal on the right, below the small fifth anal, and

extends from the right superior edge of the primibrach on the left nearly to the top of the second secundibrach. Fourth anal pentagonal, width one-third the height, wedge-shaped on the left, tapers somewhat to the right, adjacent to the second anal below, to the second and third secundibrachs on the right, to the sixth anal above, and between the third and fifth anals on the left. This specimen actually possesses only six plates in the anal interray, but the superior facet of the third anal and the upper left facet of the fourth anal indicate that a very small quadrangular plate, the fifth anal, was formerly present. It lay above the third anal, to the left of the fourth anal, below the sixth anal, and to the right of the second and third secundibrachs. An almost equilateral triangular plate, the sixth anal, forms the apex of the anal interray and truncates the fifth and fourth anals below.

Remarks.—There are a number of similar species of *Zeacrinus*. Their chief differences lie in the arrangement, shape, and size of the plates of the anal interray. *Bifurcatus* McChesney, *chesterensis* Sutton and Wagner, *doverensis* Miller and Gurley, *merope* Hall, *obesus* Miller and Gurley, *wortheni* Hall, *brevilatus* Sutton and Hagan, and *fusiformis* Sutton and Hagan are similar in that each possesses two extra quadrangular primibrachs between the cuneiform axillary primibrach and the radial of the anterior ray. Most of these species differ in the number of plates in the anal interray, but some of them are similar in this respect (see table), e.g., *Z. doverensis*, *Z. fusiformis*, and *Z. brevilatus*. These three species are distinguished on the basis of the arrangement, size, and shape of the plates in the anal interray (text figs. 7–9).

Z. brevilatus possesses a pentagonal radianal, which enters farther into the dorsal cup than does the hexagonal radianal of *Z. doverensis*. The second anal plates of *Z. brevilatus* and *Z. doverensis* are of different shapes. The third anal in *Z. brevilatus* is pentagonal and more elongate than the low, wide, quadrangular plate of *Z. doverensis*. The last three anals extend entirely across the anal area in *Z. doverensis*, whereas the opposed arrangement is maintained in *brevilatus* except for the triangular apical piece. Plate five of the latter is the smallest plate of the anal interray.

Two of the new species, *Z. brevilatus* and *Z. fusiformis*, are very similar, but the chief difference is in the anal interray, where the apical plate of the former is triangular and of the latter quadrangular (text figs. 7, 8). The pentagonal radianal of *Z. fusiformis* is wider distally than the radianal of *Z. brevilatus*, which has a more elongate shape due to its narrowness. Anal *x* of both species is six-sided although of different shape. Both second anals are hexagonal, but the lateral edges of the narrower plate of *Z. brevilatus* are more nearly parallel. The upper facets of the first and second anals of *Z. brevilatus* are almost equally elevated, but the upper surface of the first anal is set somewhat below and to the left of the second anal in *Z. fusiformis*. The pentagonal fourth anal of the latter is higher than wide, whereas that of the former is wider than high.

Horizon and locality.—The holotype of *Z. brevilatus* was collected from the Chester series (Glen Dean) at Sloans Valley, Kentucky. It is now number 19126 in the Gurley Collection in Walker Museum.

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JOURNAL OF PALEONTOLOGY, VOL. 13, NO. 1, PP. 96–99, PL. 16, JANUARY, 1939

FOSSIL MOLLUSKS PRESERVED AS CLAY REPLACEMENTS, NEAR PONTOTOC, MISSISSIPPI

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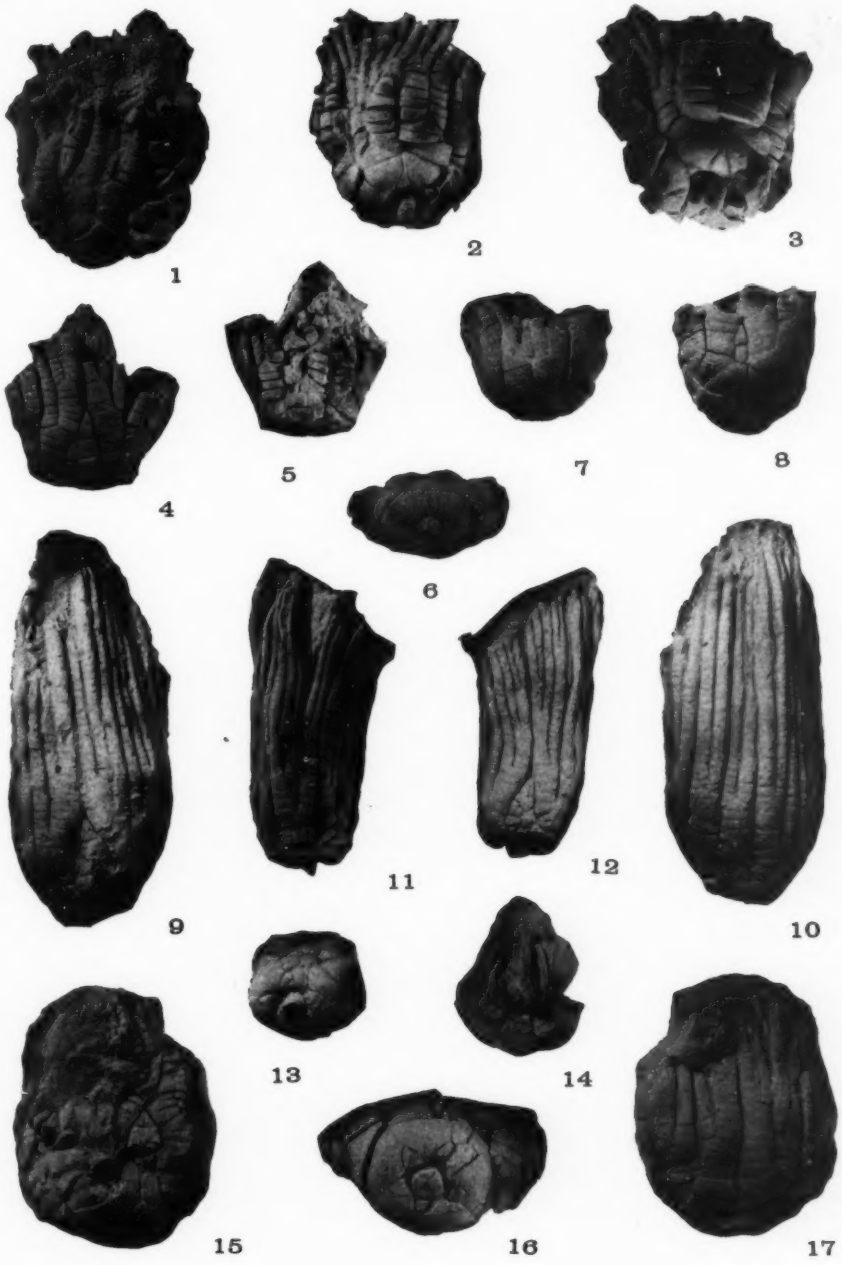
THE REPLACEMENT of the calcium carbonate of fossil molluscan shells by a clay substance is an unusual phenomenon, and the discovery of a bed of shells in that state of preservation in a railroad cut half a mile south by west of Pontotoc, Miss. (pl. 16, fig. 2), is worthy of record. I first examined the section exposed in this cut in September 1910 at which time an unsuccessful attempt was made to collect the fossils. Subsequent visits were made to the locality in June 1915 in company with Drs. E. N. Lowe and Bruce Wade, and in June 1936 and again in March 1938 in company with W. H. Monroe. At the times of the last two visits the materials composing the lower part of the section as high as the Cretaceous-Eocene contact were concealed by talus and vegetation. The lower part of the section described below is based, therefore, on observations made during the first two visits.

EXPLANATION OF PLATE 15

All figures natural size unless otherwise indicated

FIGS. *1–3—Zeacrinus brevilatus* Sutton and Hagan, n. sp. Posterior, anterior, and basal views of the holotype; *1*, and *3* somewhat enlarged. (p. 92)
4–6—Zeacrinus acuminatus Sutton and Hagan, n. sp. Posterior, anterior, and basal views of the holotype. (p. 90)
7, 8—Zeacrinus lineatus Sutton and Hagan, n. sp. Anterior and posterior views of the holotype. Specimen somewhat distorted. (p. 89)
9, 10—Zeacrinus fusiformis Sutton and Hagan, n. sp. Posterior and anterior views of the holotype. (p. 91)
11–13—Zeacrinus lanceolatus Sutton and Hagan, n. sp. Anterior, posterior and basal views of the holotype. (p. 87)
14—Zeacrinus sp. View of ventral sac. Note the two series of plates of the posterior interray, the outer one of which continues nearly to the top of the sac. The other interradial areas contain only one series of plates. The lower interradial plates of the posterior area, which possess flat exteriors, are the ones herein designated radianal and anal plates.
15–17—Zeacrinus trapeziatus Sutton and Hagan, n. sp. Posterior, basal, and anterior views of the holotype, a somewhat crushed specimen. (p. 88)



Sutton and Hagan, Mississippian Crinoids

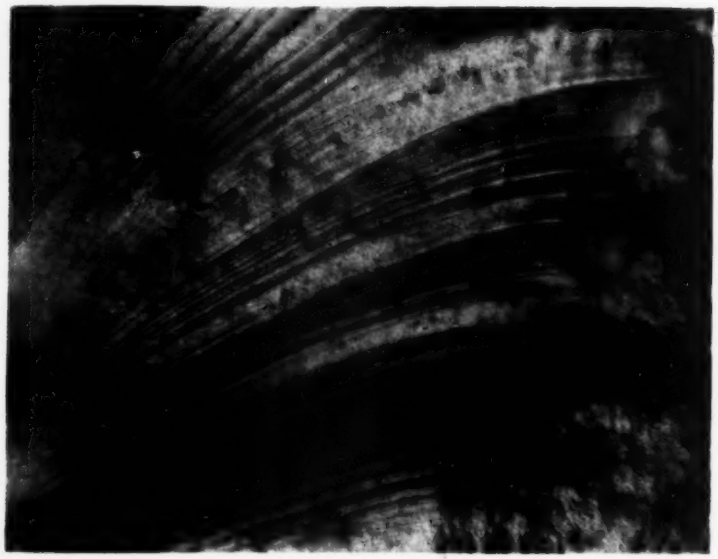


FIGURE 1. Fragment of a bivalve molluskan shell replaced by clay (beidellite), x 260, through crossed nicols. The minute structure becomes visible because of the different optical orientation of the clay crystals in the different lamellae.

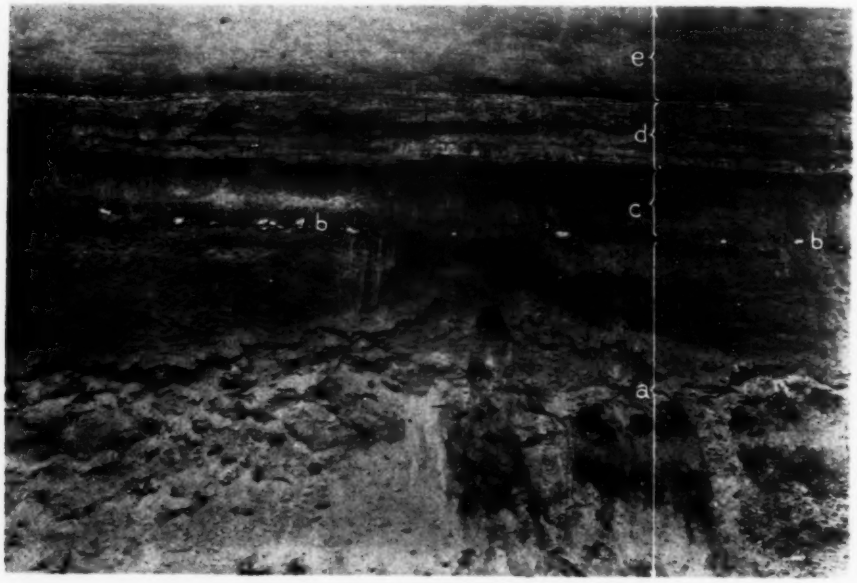


FIGURE 2. Part of section in railroad cut half a mile south by west of Pontotoc, Miss. *a*, Upper part of bed 2 (Owl Creek formation). *b*, Cretaceous-Eocene contact, marked by white clay pebbles. *c*, Bed 3 (Eocene), containing fossil shells replaced by clay. *d*, Bed 4. *e*, Lower part of bed 5.

Stephenson, Shells replaced by clay

SECTION IN CUT OF GULF, MOBILE AND NORTHERN RAILROAD, HALF A MILE SOUTH BY WEST OF THE STATION AT PONTOTOC, MISS.

	Feet
Eocene (Clayton formation of Midway group):	
5. Deep-red weathered ferruginous sand, becoming brown and grading into grayish sand below; in gullies cutting this material were observed numerous loose fragments of concretionary ironstone, some with poorly preserved impressions of molluscan fossils, among which were recognized *Venericardia* sp. and *Turritella* aff. *T. mortoni* Conrad; two specimens of *Hercoglossa ulrichi* (White) were collected loose in the gullies	25
4. Thin-bedded and laminated, fine micaceous sand and clay, sand predominating, projecting slightly due to relatively greater resistance to erosion	4
3. Coarse, loose, yellowish sand with an occasional glauconite grain; at the base are chunks of mechanically derived light-gray argillaceous sand and sandy clay up to 1 foot in length; contains many mechanically derived Cretaceous fossils preserved as soft clay replacements; recognized *Glycymeris* sp., *Crassatella ripleyana* Conrad, *Cardium* (*Criocardium*) *tippanum* (Conrad), *Turritella* n. sp. (with 2 spiral lirae), and *Pugnellus* sp.	3–4
Unconformity	
Upper Cretaceous:	
2. Owl Creek formation (southward extension of upper part): Mottled grayish to purplish glauconitic ("pepper and salt") sand, irregularly indurated in its middle part to calcareous sandstone; the latter contains *Ostrea tecticosta* Gabb, *Gryphaeostrea vomer* (Morton), *Exogyra costata* Say, and *Pecten simplicius* Conrad	25
1. Prairie Bluff chalk (northward extension of lower part): Light gray, strongly calcareous sandstone poorly exposed in ditch	1+
Total	58+

The fossil shells preserved as clay replacements in the basal sand of the Clayton formation are in a good state of preservation and are easily removed from the loose sand matrix. They are, however, very soft and easily damaged. The fresh clay composing them is pale greenish and of dull waxy luster; the clay contains a large percentage of water, which, on exposure to the air, quickly evaporates, causing the clay to check and shrivel to thin, flaky fragments that preserve little or no semblance of the original shell form. A few of the fossils were successfully transported to Washington packed in damp sand in an airtight container.

The replacement of the calcium carbonate by clay must have taken place subsequent to the reworking of the shells from their original stratum in the underlying Owl Creek formation, for obviously they could not have withstood the mechanical process of redeposition in their present soft condition. The Cretaceous bed from which the shells were reworked was not seen in the vicinity of the railroad cut, but it must have been near at hand, for the shells show little evidence of wear by transportation. Presumably the bed was overlapped for a short distance by the transgressing Midway sea.

Since the discovery of this bed of reworked shells preserved as clay replacements, W. H. Monroe[1] has observed it in three other exposures distributed along the strike in Pontotoc and Chickasaw counties, a total distance of 11 miles, as follows:

South-facing slope of a small valley on old Mississippi Highway 15, sec. 17, T. 10 S., R. 3 E., Pontotoc County.

Mississippi Highway 15, 0.4 mile south of South Prong of Chiwapa Creek, sec. 5, T. 11 S., R. 3 E., Pontotoc County.

Road cut on east-facing slope of Chookatonkchie Creek valley, 0.4 mile east of Mississippi Highway 15, sec. 4, T. 12 S., R. 3 E., Chickasaw County.

Monroe says:

At the locality in Chickasaw County the shells are much broken up, and the replacement is not complete, for only part of the shells have been changed to clay, the others still retaining their original calcium carbonate. All are cemented together into large, concretionary masses.

Dr. Clarence S. Ross, of the Geological Survey, through whose courtesy an analysis was made for the author, has kindly studied the replacing clay and the enclosing sand

[1] Oral communication.

under the microscope. His description is as follows:

A microscopic examination of the shell material from near Pontotoc indicated that it was made up of an unusually pure clay mineral of the montmorillonite group. The purity, and the unusual type of replacement represented indicated the desirability of a detailed study. The material was prepared for analysis by carefully scraping away the sandy matrix and adhering ferruginous film of the replaced shell, and this gave an exceedingly pure sample of clay. The material was then analysed by J. G. Fairchild of the United States Geological Survey, whose results are given below:

CHEMICAL ANALYSIS OF PONTOTOC CLAY MINERAL

SiO_2	46.95
Al_2O_3	27.26
Fe_2O_3	2.26
FeO	.32
MgO	1.39
CaO	None
Na_2O	.20
K_2O	.36
H_2O-	11.10
H_2O+	10.55
TiO_2	None
P_2O_5	.03
MnO	.01
	100.43

This analysis confirms the mineral as a member of the montmorillonite group. The ratio of $Al_2O_3+Fe_2O_3$ to SiO_2 is 1:2.772, which indicates a high alumina content, the normal ratio for montmorillonite being 1 Al_2O_3 to 4 SiO_2, after allowing for the magnesian member of this mineral group. Thus the mineral corresponds to beidellite, the high alumina member of the group. The presence of MgO in excess of other bases is normal, but the total absence of CaO is rather unusual. Other bases and the water content are present in about normal proportions.

A microscopic examination shows numerous areas where a uniform orientation of the clay material permits a determination of the optical properties. The mean index of refraction is about 1.53, which is a little high for minerals of this group, but is, no doubt, due to the iron content. The birefringence is about like that of micas; the mineral is biaxial; and the optical character is negative. In thin sections many of the specimens show the very fine grained lamellar structure that characterizes shell material, and shows that replacement has preserved the original shell structure with remarkable exactness. (See pl. 16, fig. 1.)

The shells, as previously pointed out, have been reworked, and replacement has occurred subsequent to their deposition in the sand. This sand is made up mainly of angular to subrounded grains of quartz that average about 0.35 of a millimeter in diameter, but which are extremely variable in size. These are coated with an admixture of highly ferruginous clay and limonite. That is, calcareous shells while enclosed among sand grains coated with a small proportion of iron-rich material, were replaced by an extremely pure clay mineral. The resulting mineral, contrary to all expectations, contains no calcium and only a moderate amount of iron.

The replacement of calcareous shells by clay material raises a question as to the chemistry of the process. It is evident that clay forming material must have been introduced into the shells from the outside and solutions of some kind are the only means for such replacement. Clay is a material that, no doubt, at times is transported in colloidal solutions. However, colloidal solutions are chemically inactive, have small power of penetration, and are especially ineffective for the removal of replaced material. It, therefore, seems probable that the calcite shells from near Pontotoc were replaced by cool solutions carrying the necessary elements for the formation of clay in true chemical solution. These solutions dissolved and removed the $CaCO_3$ of the shells, and at the same time they were introducing Al_2O_3, SiO_2, a little Fe_2O_3, MgO, and unimportant amounts of other elements.

Dr. P. S. Nutting of the Geological Survey has kindly made a thermal study of the replacing clay. The results of this work show that the dehydration curve is typical of minerals of the montmorillonite group.

A bed of reworked Cretaceous shells in a different state of preservation, but occupying the same stratigraphic position at the base of the Eocene, is exposed about 14 miles north of Pontotoc on Mississippi State Highway 15, $3\frac{1}{4}$ miles south of New Albany, Union County. Here the shell bed is 2 to 3 feet thick and is a greenish-gray sandy, coquinalike, friable limestone containing in the matrix between the shells great numbers of small yellow and brown limonitic oolites with polished surfaces; there are also a few small gray spherical grains, some of which are composed of solid crystalline calcite, and some forming a shell of calcite enclosing sand matrix. The basal 2 to 6 inches of the bed is unconsolidated. The fossils are preserved in part as calcium carbonate and in part as molds; however, here and there among the shells the calcium carbonate has been incompletely replaced by clay (confirmed by C. S. Ross), showing that the same replacement process operated here, though less completely than at the other

localities farther south. The fossils include *Exogyra costata* Say (variety with narrow costae), *Crenella serica* Conrad, *Trigonia angulicostata* Gabb, *Turritella* n. sp. (with 2 spiral lirae), and many others. The shell bed is separated from underlying Cretaceous strata of the Owl Creek formation by a gently undulating, sharp, unconformable contact. The bed is immediately overlain by 5 feet of sandy, nodular limestone, also containing the limonitic oolites, and carrying the Midway Eocene species *Ostrea pulaskensis* Harris.

A sample of the coquinalike rock was examined by Dr. Charles Milton in the Chemical Laboratory of the Geological Survey, who says:

The sample is a mass of shells, mainly mollusks, cemented by a calcareous sandy matrix in which are numerous yellow to brown ovoid particles, the largest smaller than a small pinhead.

These particles are (1) grains of quartz or feldspar, thinly coated with limonite, (2) foraminifera whose chambers and exterior are filled and coated with limonite, and (3) solid masses of limonite, presumably after glauconite, though marcasite and siderite are also possible. On roasting the particles become magnetic, give the usual chemical tests for iron, and insignificant tests for phosphate.

Optically the particles are blackish brown, opaque, and isotropic, for the most part; glauconite is present but rare in the sample.

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TURRITELLA KELLUMI, NEW NAME FOR TURRITELLA SUBTILIS STEPHENSON

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THE NAME *Turritella subtilis* was proposed in 1926 by L. B. Kellum (1) for a species preserved as an external mold in the Castle Hayne marl, of Jackson Eocene age, at Wilmington, North Carolina. At the time Kellum's paper was in press, and unaware of the new names he was proposing, I used the same name for a species from the Upper Cretaceous Peedee formation (2) exposed in the new Rocky Point quarries one mile northeast of Rocky Point station, Pender County, North Carolina. My material was collected by Dr. Kellum. As the name proposed by Kellum was published before mine, I rename the Rocky Point species *Turritella kellumi*.

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JOURNAL OF PALEONTOLOGY, VOL. 13, NO. 1, PP. 100–102, 2 TEXT FIGS., JANUARY, 1939

CAMPANILE GREENELLUM, A NEW SPECIES FROM THE EARLY EOCENE OF CALIFORNIA

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WORK during the construction of a new highway has recently necessitated a cut through conglomeratic beds which occur between San Pedro Point and Devils Slide some twelve miles south of San Francisco, California. Sandstones underlying the conglomerates north of San Pedro Point have yielded a poorly preserved fossil, which Dr. F. M. Anderson identified as a portion of a *Crioceras*-like ammonite (1). This specimen was found by Dr. Olaf P. Jenkins, Chief Geologist of the Division of Mines of the State of California. Some pebbly conglomerates in this general area have been referred to the Martinez, lower Eocene, by Dickerson (2) but the relationship of his fossil locality to the present one has not yet been determined with certainty.

Passing through this region one day, Mr. M. H. Green, supervisor for the Works Progress Administration, paused to examine the material in the road cuts and that which had been excavated and thrown along the side of the road near the ocean cliff between San Pedro Point and Devils Slide. Miss Susanne Scheuer, artist with the Works Progress Administration, noticed among the loose material the shell of a fossil gastropod, which Mr. Green later submitted to us for identification. Even a cursory examination revealed that this represented a new species of *Campanile*, very close to the species *claytonense* from the Midway group of Alabama. In the light of recent discussions regarding the exact age of the Midway group (3) the present new species is of more than usual interest. The similarity of our species to one which occurs in the Midway would seem to bear out Dickerson's suggestion that the Martinez of the west coast of America might be regarded as approximately equivalent to the Midway of the Gulf Coast. Provisionally we refer the Martinez to the lower Eocene.

Nelson (4) has mentioned the occurrence of casts of *Campanile* in the lowest bed in the vicinity of Cachuma Creek in the Santa Ynez quadrangle, Santa Barbara County, California. Two echinoids, *Amblypygus subhemisphericus* Israelsky and *Linthia sanrafaelensis* Israelsky were found associated with *Campanile* at that locality. These apparently occur in the beds now referred to the Sierra Blanca limestone, of middle or upper Eocene age. Woodring (5) also has mentioned the occurrence of "giant Cerithia" in the Eocene in the San Rafael Range near the eastern border of the Mt. Pinos quadrangle.

We here express our appreciation to Mr. M. H. Green for the opportunity to study the specimen described as new herein. We also acknowledge helpful advice and suggestions by Dr. O. P. Jenkins regarding the field relations of the sedimentary beds in the vicinity of San Pedro Point; also suggestions from Mr. Frank B. Tolman regarding cerithids in the Eocene of southern California. The photographs were made by Mr. Frank L. Rogers. These photographs are the result of work accomplished during a government Works Progress Administration project.

CAMPANILE Bayle, 1884

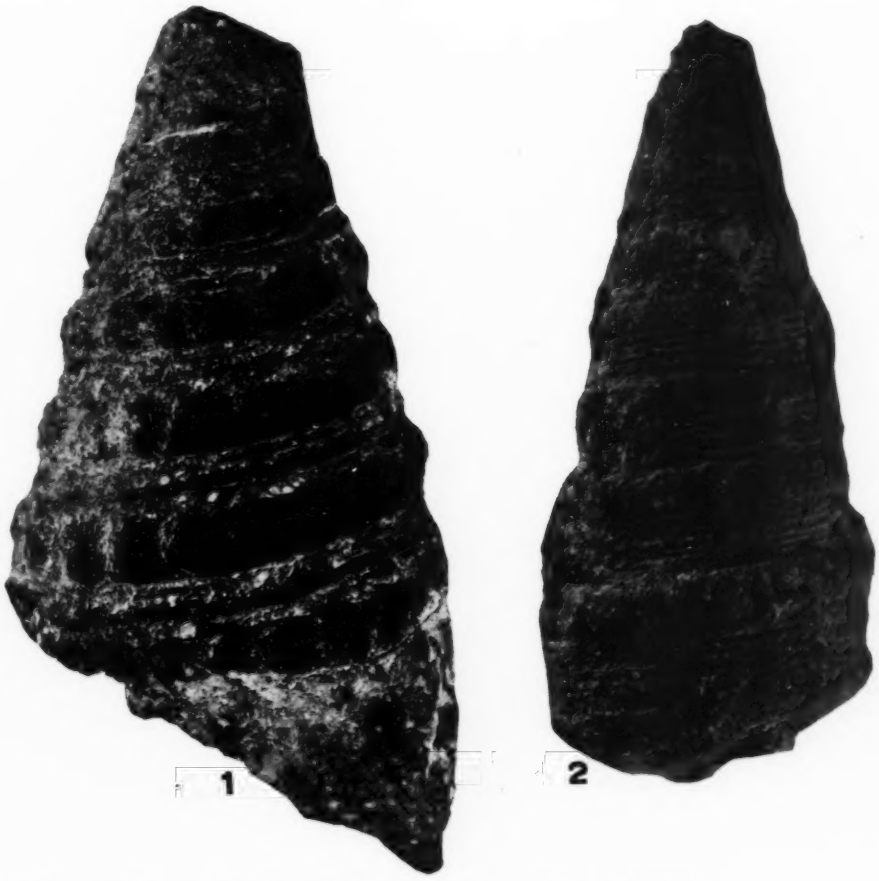
Campanile BAYLE, in FISCHER, *1884*, Manuel de Conchyl., p. 680. Two species cited: "*C. laeve*, Quoy et Gaimard. Australie" and "*C. giganteum*, Lamarck"; Eocene.—COSSMANN, *1889*, Soc. royale malacol. Belgique, Annales, vol. 24, (Cat. illustré, fasc. 4), p. 25. "Type: *C. giganteum*, Lamk."—COSSMANN, *1906*, Essais de Paléontologie comparée, vol. 7, pp. 71–73. "G. Type: *Cerith. giganteum*, Lam. Eoc."—BOUSSAC, *1912*, Annales Hébert, vol. 6, p. 19. Cossmann's designation of *Campanile giganteum* Lamarck, as type, cited.—COX, *1930*, Foss. fauna of Samana Range, pt. 8, Palaeontologia Indica, new Ser., vol. 15, p. 148. Cossmann's designation of type cited.

Campanile includes a group of giant cerith-

ioids and is a characteristic genus of the ancient Tethyan sea. Cossmann cited the range as Maestrichtian, upper Cretaceous to Recent, the possible modern representative being *C. laeve* Quoy and Gaimard, in Australia. Oppenheim (6) has discussed the genus *Campanile* and many of the early Tertiary cerithids. As pointed out by Oppenheim the species *laeve* probably belongs to a different subgenus. A paper by Boussac (7) presents the results of studies of the development of the Eocene cerithids in France. Cossmann cited two species of *Campanile* from the Paleocene, *Cerithium coemansi* Briart and Cornet in Europe and *Cerithium claytonense* Aldrich in the Midway of southeastern United States. To the early Eocene forms we now add a new species *Campanile greenellum.*

CAMPANILE GREENELLUM Hanna and Hertlein, n. sp.
Text figure 1

Shell elongate conic, imperfect but with about 8 whorls. The top of each whorl ornamented by a band of elevated nodes, there being about 22 on the last whorl; below each band of nodes there are three revolving cords separated from each other and from the nodose band above and below by incised lines. Length (incomplete) approximately 95 mm, greatest width 64 mm.



FIGS. *1—Campanile greenellum* Hanna and Hertlein, n. sp. Holotype (7233).

2—Campanile claytonense Aldrich. Hypotype.

Type.—Holotype 7233 (Calif. Acad. Sci. Paleo. Type Coll.), from San Mateo County, California, south of San Francisco, in a blackish-gray pebbly conglomerate used in road building, between San Pedro Point and Devils Slide (U. S. Geological Survey Topographic Sheet, edition of June, 1915, reprinted 1930). This locality is on cliffs along California State Highway no. 1, one-half mile north of Devils Slide and about 1.5 miles south from where the road to Tobin Station branches to the west.

Campanile greenellum resembles closely *Campanile claytonense* Aldrich (8) but is less tapering in form. There are three raised spiral ridges below the nodulous band separated by incised lines. On *claytonense* there are four or five incised lines compared to three or four on the California species. Perfect specimens may, however, show the above differences to be even less pronounced.

Miss Winnie McGlamery of the Alabama Museum of Natural History kindly loaned us a specimen of *C. claytonense* from the lower Eocene of Furman, Alabama. This specimen, illustrated by figure 2 has about 8 whorls, the apex incomplete, the length 119.4 mm, maximum width of the body whorl 56.2 mm. The top of the last whorl has 12 nodes, one side was worn and probably originally had about 6 more, so that the complete whorl probably had 16 to 18 nodes. Below the row of nodes there are 5 to 6 raised lines with a few very fine lines in the interspaces. The base is unornamented.

Boussac has discussed and illustrated thirteen species and one subspecies of *Campanile* mostly from the Eocene of the Paris Basin. The only ones bearing a general resemblance to the California species are *C. paratum* Deshayes and *C. benechi* Bayan, but the similarity is very much less pronounced to these than it is to *claytonense* from Alabama.

This species is named for Mr. M. H. Green, supervisor for the Works Progress Administration, who presented the type specimen to us.

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HELICOPRION IN THE ANTHRACOLITHIC[1] (LATE PALEOZOIC) OF NEVADA AND CALIFORNIA, AND ITS STRATIGRAPHIC SIGNIFICANCE

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ABSTRACT—The discovery of two new species of the fish *Helicoprion*, one from the Humboldt Range of northwestern Nevada, and the other from the northern Sierra Nevada of California, both in formations of long-supposed Mesozoic age, has led to a review of the other occurrences of the genus. The stratigraphic restriction of *Helicoprion* to the Uralian and Artinskian stages impels the assignment of these strata of Nevada and California to the Anthracolithic.[1] The new species *Helicoprion nevadensis* and *H. sierrensis* are described.

THE SPIRAL of *Helicoprion* has been one of the most enigmatical of fossils, and in the past has been the subject of much debate as to what part of the selachian anatomy it belongs. In spite of the widespread taxonomic and comparative anatomical interest this genus has afforded, it has received little attention from the stratigraphic point of view. This lack of interest has not been wholly unjustifiable, for only a few specimens from still fewer localities have been reported to date.

That *Helicoprion* is rarely mentioned in American literature is to be expected, for, with only one exception, those few previously reported species (of known locality) are confined to the Eastern Hemisphere, where they are known from the Anthracolithic of Russia, Central Asia, Japan, India, Indo-China, and Australia. Of the two recorded American occurrences, one is that of an incomplete and imperfect specimen of unknown locality reposing in the Tufts College Museum in Boston. Eastman (1902) based his genus *Campyloprion* upon this specimen, but Karpinsky (1912) refers it to *Helicoprion*. The other includes several specimens of *H. ferrieri* (Hay) from a single horizon in the Phosphoria formation—one from a locality near Montpelier, Idaho, and others from nearby Thomas Fork, Wyoming (Hay, 1907 and 1909).

The discovery of *Helicoprion* in similar stratigraphic horizons in northwestern Nevada and northeastern California has led to a review of other occurrences of the genus—a review that has shown its world-wide geographic distribution, together with its restricted stratigraphic range.

These discoveries are significant, not only because *Helicoprion* proves important as a stratigraphic index, but also because they throw new light on the paleogeography and sequence of events in western North America during the time of the deposition of the rocks in which these fossils occur.

HELICOPRION BIOZONE

The genus *Helicoprion* was based by Karpinsky (1899) on specimens of selachian dentition from a quarry in Artinskian limestone near the town of Krasnoufimsk on the western flank of the Ural Mountains.

In the Russian Anthracolithic the genotype, *H. bessonowi*, is restricted to the very limited Krasnoufimskian horizon of the Artinskian stage. Undescribed Artinskian occurrences of *Helicoprion* in U.S.S.R. are mentioned by Licharew (1937)—one from the Cajgadsinskji horizon in the southern Urals, and another from southeastern Central Asia, south of the city of Osch.

Two specimens of the genus are reported from Russian rocks of Uralian age. Karpinsky (1922) describes *H. ivanovi* from the

[1] In view of the world-wide diversity of usage of the terms "Carboniferous" and "Permian," the writer here (and elsewhere) employs the term "Anthracolithic," which unit includes all the late Paleozoic from the base of the Dinantian stage (Mississippian) upward.

Omphalotrochus zone of the Uralian, and Licharew (1937) mentions an undescribed specimen from Uralian rocks of the Donetz region. Unfortunately, this last specimen has been lost.

In Japan, a specimen of *H. bessonowi* is reported by Yabe (1903) from a "*Fusulina*" limestone near Hanawa on the Waterasegawa River. From the same limestone at nearby localities he describes the occurrence of a variety of "*Fusulina*" *japonica* Gümbel and a new species of *Neoschwagerina*, similar to *N. craticulifera* (Schwager). On the basis of this association, Yabe assigns this *Helicoprion*-bearing limestone to the Permian [Artinskian or later], rather than to the Upper Carboniferous in which it had previously been placed.

According to Gubler (1937), *Pseudofusulina japonica* is found in the Lower, Middle, and at the base of the Upper Permian [Artinskian or above] of the Far East. But he gives assurance that if the Japanese neoschwagerine belongs to the group of *N. craticulifera* (see Gubler, 1935), it is restricted to the Lower Permian [Artinskian]; and the number of secondary septa clearly indicates that it does belong to that group. That age, of course, is only to be expected, in view of the identity of the Japanese *Helicoprion* and *H. bessonowi* from the type Artinsk stage.

Helicoprion sp. is reported by Koken (1901) from the Chideru beds of the Upper *Productus* limestone of the Salt Range in India. The age of none of the *Productus* limestone formations, in terms of the Russian section, has ever been universally agreed upon, although no authority has held that the Chideru beds are older than Artinskian. One of the most significant of recent correlations is that of Grabau (1931) who, on the basis of a study of 34 brachiopod species common to both the Ural-Timan and Salt Range sequences, correlates the Upper *Productus* limestone with the Artinskian and lower Kungurian. It is to be noted that this correlation by Grabau is in accord with the earlier findings of Tschernyschew (1902).

In Indo-China, Hoffet (1933) reports a specimen of *Helicoprion* from the Houeï Nam Cam limestone north of Sarvane in the province of Laos. Hoffet states that this limestone rests with perfect concordance upon upper Uralian beds which contain *Pseudofusulina japonica*, *Linoproductus cora*, and *Euomphalus*.

In addition to *Helicoprion*, the Houeï Nam Cam limestone carries the following "Permian" fauna: Nautiloid cf. *Tainoceras* sp., *Orthoceras cribosum* Geinitz, *Strophalosia plicatifera* Chao, *Aviculopecten* cf. *A. hiemalis* Salter, *Murchisonia* (*Glyphodeta*) *permeana* Jakolew, *Nucula kazanensis* De Verneuil, *Pleurotomaria* sp., *Naticopsis* sp., *Loxonema* sp., *Conularia* cf. *C. tenuistriata* McCoy, and fish teeth and skeletal remains.

Although Hoffet (1938) is not yet prepared to designate the precise age of the Houeï Nam Cam limestone, it is clear that it is post-Uralian; and in view of its concordance with the underlying Uralian strata, together with the general aspect of its fauna, an Artinskian age for these *Helicoprion*-bearing strata seems most probable.

The stratigraphic position of the Western Australian occurrence of *Helicoprion* (*Edestus davisi* Woodward, 1886) is unfortunately unknown. The specimen (a detrital concretionary fragment) was collected "in the valley of the Arthur River, an affluent of the Gascoyne . . . about 130 miles in direct distance from the sea." It is known that the Arthur River passes through a region of Anthracolithic rocks from which this specimen was doubtless derived, but otherwise it has not been allocated.

Present knowledge regarding this specimen is summed up by Raggat and Fletcher (1937), who state:

> Mention may be made of the fossil shark *Helicoprion?*. Great stress has been laid upon the importance of this fossil [Schuchert, (1928); David and Süssmilch (1931)], but the facts about it unfortunately are that it was not found *in situ*, and that it is practically impossible to identify it beyond doubt. Judging by the lithology and matrix and the fact that the specimen was picked up somewhere on the Arthur River, Raggat would hazard the guess that it came from the Byro stage. If so, it is Permian; but in view of the uncertainty attaching to the specimen no useful conclusions can be drawn from it.

As stated above, the only previously described American species of *Helicoprion* of

known locality is *H. ferrieri* (Hay)[2] from the Phosphoria formation of Idaho and Wyoming. Although the age of the Phosphoria, in terms of European stages, has never been precisely established, there can be no question that it falls within the Eurasian range of *Helicoprion*.

Girty (Mansfield, 1927) regards the Phosphoria as contemporaneous with "the highest Paleozoic beds of Alaska," the fauna of which has been examined by Holtedahl, who expressed the opinion that it belongs to the Artinskian.

King (1931) has shown the faunal likeness of the Phosphoria to the Word formation of West Texas; and Gordon (1937), who is making a study of the Gerster formation of northeastern Nevada (a western facies of the Phosphoria), is convinced of the contemporaneity of the Gerster, Phosphoria, Word, Nosoni of California, and the so-called "Schwagerinenkalk" of the Ural section. Unfortunately, however, the position of the "Schwagerinenkalk" within the Russian sequence is uncertain. Whether it is to be placed in the Uralian or Artinskian remains to be established. Nevertheless, that the Phosphoria belongs to one or the other of these stages seems inevitable.

On the basis of the above summation of present knowledge, therefore, it may be stated that the *Helicoprion* biozone does not extend below the *Omphalotrochus* zone of the Uralian stage, nor above the top of the Artinskian. Thus, the genus is to be regarded as a zone fossil, confined to a limited portion of the Anthracolithic.

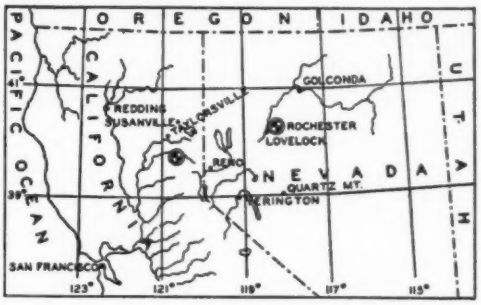

FIG. 1.—Index map of northern Nevada and northern California showing localities of *Helicoprion* and other areas mentioned in the text.

HELICOPRION IN NEVADA

The dominantly eruptive Koipato "formation" of the Humboldt Range in northwestern Nevada has yielded to date but one fossil—a well-preserved *Helicoprion* mold. The specimen is from a stratified tuff member, intercalated about 4,000 feet below the top of the Rochester trachyte, near the townsite of the mining camp of Upper Rochester. (See map, fig. 1.)

The earliest attempt to define and map the formations of the Humboldt Range was made by King (1878), who described the Koipato "group" as consisting of a vast thickness of "quartzitic and argillaceous beds" or "schists and porphyroids." King assigned the Koipato to the Triassic because he found it to be directly overlain by "limestones and quartzitic beds [Star Peak group], characterized by fossils of the St. Cassian Alpine Trias age."

Ransome (1909) refers to the Koipato "formation" as the "lower division of the Triassic." He further states that its rocks consist of "volcanic flows, mostly rhyolitic but including also andesitic lavas, associated with tuffs, conglomerates, grits and limestones."

Knopf (1924), in his discussion of the "Triassic" formations of the Rochester district, cites Smith (1914) to show that the Star Peak formation is of Middle and Upper Triassic age; and from this he concludes that the immediately underlying Koipato

[2] A previously unrecorded specimen of *H. ferrieri* reposes in the collection at Stanford University (Stanford Univ. Paleo. Type Coll., no. 5093); but, unfortunately, its locality label has been lost. It seems highly probable, however, that this fossil comes from the Phosphoria formation of southeastern Idaho or westernmost Wyoming, for the following reasons: The Stanford specimen belongs to the well-known Phosphoria species; the matrix consists of an impure, black limestone with a strong fetid odor when freshly broken (Mansfield, 1927); the limestone is phosphatic; this rock specimen carries brachiopods, nuculidlike lamellibranchs, and *Omphalotrochus ferrieri* Girty, which assemblage is so characteristic of the Phosphoria formation; and finally, specimens of the matrix have been compared with the limestone surrounding specimens of *Helicoprion ferrieri* from near Montpelier, Idaho, by Mr. E. P. Henderson, U. S. National Museum, who pronounces them to be the same lithologically.

AGE		FORMATION	THICKNESS	DESCRIPTION
TRIASSIC	MIDDLE TRIASSIC	STAR PEAK FORMATION (LOWER PART)	1000′+	Conglomerate and sandstone at base, grading upward into calcareous shale and bituminous limestone. Limestone carries assemblage of Parapopanoceras zone (J.P. Smith).
		DISCONFORMITY		
ANTHRACOLITHIC	KUNGURIAN OR ARTINSKIAN	WEAVER RHYOLITE	3000′+	Rhyolitic lavas with small volume of intercalated tuff, shale and breccia.
		NENZEL RHYOLITE BRECCIA	600′–	Rhyolite breccia, generally devoid of bedding, but locally containing banded, fine-grained, lenticular beds of tuff.
	ARTINSKIAN OR URALIAN	ROCHESTER TRACHYTE	5000′+	Felsitic lavas, volcanic breccia and tuffs. Pyroclastic portion probably exceeds lava in thickness. (Helicoprion occurs in tuffaceous shale, about 4000 feet below the top of the formation.)
	?	LIMERICK KERATOPHYRE	5000′+	Keratophyric lavas intercalated with tuff and breccia. (Base unknown.)

TABLE 1. Columnar section showing relationships of the Anthracolithic (Koipato) volcanic series of the Humboldt Range, Nevada. (Modified after Smith, Knopf, and Jenney.)

"is of Middle Triassic age at least, but it may be older, though this is regarded as highly improbable."

Others to concur in the opinion that the Koipato rocks are of Triassic age are Jones (1915), Schrader (1914), Kerr and Jenney (1935) and Jenney (1935).

The discovery of *Helicoprion* in the Rochester trachyte[3] precludes the possibility that all this 15,000-foot series of rocks below the Star Peak are of either Lower or Middle Triassic age. (See table 1.) The stratigraphic restriction of that genus to the Uralian and Artinskian stages necessitates the assignment of at least the Rochester trachyte to the Anthracolithic. In addition, it is likewise necessary to regard the Limerick keratophyre as belonging to the late Paleozoic since Knopf (1924) and Jenney (1935) agree that these two formations are clearly contemporaneous.[4] Thus, it is evident that at least some 10,000 feet or more of the Koipato must be assigned to the Anthracolithic rather than to the Triassic, as formerly believed.

In regard to the age of the remainder of the Koipato, i.e., the Nenzel rhyolite breccia and Weaver rhyolite, which intervene between the Rochester-Limerick series and the Star Peak strata, Knopf (1924) observes that the Middle Triassic limestone is locally intercalated with the rhyolitic tuff and breccia, and what appear to be andesitic rocks. If this were true, it would appear that at least the waning stages of the Koipato volcanic epoch were contemporaneous with the deposition of the Middle Triassic limestones.

In this regard, a study has been made of the lower portion of the Star Peak formation and its contact with the underlying Weaver rhyolite at localities on both sides of the range.

On the west side of Independence Hill, in the Rochester district, the basal, noncalcareous portion of the Star Peak strata con-

[3] Because Knopf (1924) regarded Koipato as an insecure stratigraphic term, he named the Rochester trachyte and other units in its stead.

[4] Since the Limerick and Rochester units are both exposed along the axis of a faulted, southwardly plunging anticline, and since the exposures of the former are bordered on the east, west and south by the latter (see maps: Knopf, 1924; and Jenney, 1935), it would appear that the Limerick keratophyre is stratigraphically lower, rather than contemporaneous with the Rochester trachyte.

sists of 200 feet of conglomerate and sandstone, lying disconformably upon the rhyolite. Except that these basal beds are thinner by thirty feet, similar relationships occur on the south side of Fisher Canyon, on the east side of the range. Although the conglomerates at both localities are clearly derived from rhyolite, no lavas nor pyroclastics could be found in either section above the unconformity.

In further substantiation of these conclusions is the following statement by Muller and Ferguson (1937):

> At a number of localities in the West Humboldt Range, the Koapato effusives, where they are not much disturbed by faulting, are overlain disconformably, or at least without any perceptible angular discordance, by the bluish-black bituminous limestones of the Star Peak group . . . .

Thus, the presence of an unconformity between the Weaver rhyolite and Star Peak, and the absence of volcanics in the latter, forces the tentative conclusion that the entire series of Koipato eruptives should be assigned to the Anthracolithic.

Late Anthracolithic vulcanism on the Pacific Border is by no means a new suggestion. Diller (1906) has shown that violent volcanic activity accompanied the deposition of the Nosoni formation of the southeastern Klamath Mountains in northern California.

On the basis of local stratigraphy, there is no evidence to indicate the precise age of the Rochester trachyte other than the presence of *Helicoprion*. However, the similarity of the Humboldt sequence and occurrence of *Helicoprion* to that of the upper Anthracolithic of the Sierra Nevada, together with the apparent close relationship of the species from both localities, points to a similar age for both occurrences. Therefore, since the Californian beds carrying this fossil are assignable, on other evidence (see below), to the Uralian or Artinskian stages, the same position within the Anthracolithic is assumed for the Rochester formation; especially, since this assignment is in perfect accord with the known range of the genus *Helicoprion*. If this be true, the Nenzel and Weaver ejections may well represent the Kungurian stage in this region.

HELICOPRION IN CALIFORNIA

The second specimen of *Helicoprion* was collected from a glacial moraine on the southeast bank of Frazier Creek in Mohawk Valley, south-central Plumas County, California. (See map, fig. 1.)

Because this specimen has been transported, the exact stratigraphic position of its original site of deposition must forever remain in doubt. Nevertheless, within certain limits, there can be no question as to its proper stratigraphic allocation.

In order to determine the ultimate source of the rock bearing this specimen, it is first necessary to consider all the possible sources of morainal debris deposited in the vicinity of the locality of discovery. In this regard, upon field examination of the area it seems obvious that all this till has been transported and deposited by a glacier extending down the valley of Frazier Creek. Thus, the ultimate source of the detritus must lie within the Frazier Creek drainage basin.

Within this restricted area, Turner (1897) has mapped three formations, all of which he has tentatively assigned to the "Juratrias." These are: (1) rhyolite porphyry; (2) siliceous argillite; and (3) an "augitic greenstone series." The first two of these formations may be eliminated at the outset because of their marked mineralogical differences from the specimen under consideration. The greenstone series, however, which consists of several thousand feet of altered basic effusives and pyroclastics, contains numerous tuff beds, from one of which this specimen might well have been derived.

There still remains one other possible source of this boulder; namely, the Milton formation, which consists of basic tuffs similar to those of the greenstone series, together with "quartzite, fine-grained red slates, a little marble, and variegated breccia or conglomerate." The Milton directly overlies the greenstone series and was likewise assigned by Turner (1897) to the "Juratrias."

The nearest outcrop of Milton, as mapped by Turner (1897), extends northerly to a point about two miles southeast of Frazier Creek, where it is shown as disappearing beneath the moraine. The formation may well continue, however, with a northwesterly trend, across Frazier Creek, entirely covered with drift. That this may be the case is suggested by the presence of red slate (one of the notable constituents of the

Milton) in the lower Frazier moraines. Thus, it is conceivable that the *Helicoprion*-bearing rock may possibly have come from the basic tuffs of the Milton formation. That it was not derived from the Milton, however, seems more likely, since these strata are continuous to the south with what Lindgren (1900) has called the Sailor Canyon formation, and from one area of which he has collected *Daonella* and other Triassic fossils.

In any event, it is evident that in this part of the Sierra Nevada, as in the Humboldt Range of Nevada, at least the earlier, eruptive portion of the so-called "Juratrias" rocks must now be regarded as Paleozoic.

Further, if the Milton and Sailor Canyon formations are equivalent, as they must be regarded at present, and if both are of Middle Triassic age, as indicated by the presence of *Daonella* in the latter, a remarkable similarity between the California and Nevada sequences is to be noted. In both cases a great thickness of *Helicoprion*-bearing beds, consisting predominantly of rocks of volcanic origin, are superseded by Middle Triassic marine strata.

The age of these rocks carrying *Helicoprion* in California is indicated not only by the presence of that fossil alone but also by the stratigraphic relationships of these and other rocks in the Sierra Nevada. Turner (1897) shows that at the north end of the Downieville quadrangle, about fifteen miles north of Frazier Creek, the augitic greenstones are intimately associated with the Robinson formation. An association of similar (and probably the same) effusives and pyroclastics with the Robinson has been shown by Diller (1908) in the Taylorsville region about ten miles farther north. The Robinson beds, in turn, have been correlated with the Nosoni formation of the Klamath Mountains by Girty (Diller, 1908), and with both the Nosoni and the Artinskian of Russia by Smith (1895). In addition, Frech (1901) cites the occurrence of *Spirifer wynnei* in the Nosoni as indicating the presence of the Artinskian in California. On the other hand, as shown above, Gordon would correlate the Nosoni with the "Schwagerinenkalk" of the Russian sequence; and the latter may belong to the Uralian rather than the Artinskian.

In any event, through these direct and indirect correlations, it is evident that these *Helicoprion*-bearing beds of the Sierra Nevada should be assigned to either the Uralian or Artinskian; especially since the *Helicoprion* biozone elsewhere is shown to be restricted to that part of the Anthracolithic.

PALEOGEOGRAPHIC SIGNIFICANCE

The presence of a positive area in western Nevada, generally separating the late Paleozoic Pacific and interior seaways is supposed by Nolan (1928). This postulation is based upon the paucity of Anthracolithic marine strata in western Nevada, as compared with their much greater development on both the east and west. The stratigraphic relationships of some of these marine formations and their contemporary volcanics lend conclusive support to the existence of such a land mass.

As mentioned above, Diller (1906) shows the tuffaceous aspect of the Nosoni shale in the Redding quadrangle and describes intercalated felsitic lavas.[5] In passing southeastward to the Taylorsville region, the marine rocks of Nosoni age (Robinson formation, Diller, 1908) are decreased in thickness; while the associated volcanics greatly predominate. Thus a volcanic land mass toward the southeast may be postulated, although no extensive area of eruptive rocks of such age has been hitherto identified in eastern California nor in western Nevada.

The occurrence of *Helicoprion* in tuffaceous beds intercalated within thick series of effusives and pyroclastics in the Sierra Nevada south of Taylorsville and in the Koipato of the Humboldt Range in Nevada farther east proves the Anthracolithic age of these long-supposed "Mesozoic" volcanics and definitely establishes the positive area.

Further, the gradual westward thinning of the eastern Nevada limestones of Phosphoria age points to the nearness of the western shoreline of the Phosphoria epeiric sea. In northern Nevada, the westernmost

[5] In the light of the extensive late-Paleozoic vulcanism herein described, the stratigraphic relationships of the "Triassic" Dekkas andesite and Bully Hill rhyolite, which overlie the Nosoni, may bear further investigation. They too may prove to be of Anthracolithic age.

known outcrop of these marine limestones is found in the low range directly east of Golconda, in southeastern Humboldt County, where their thickness does not exceed 100 feet; whereas the thickness of contemporaneous strata is appreciably greater toward the east in Elko County.

Occurrences of volcanic rocks similar to, and possessing much the same stratigraphic

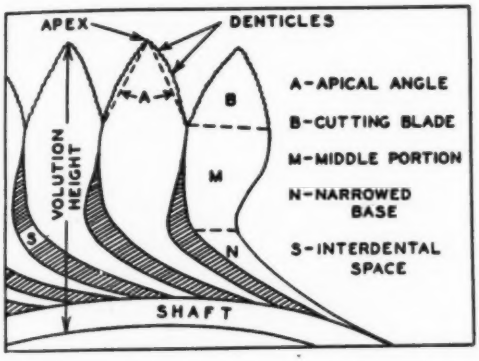

FIG. 2.—Morphologic terminology of *Helicoprion*.

relationships as the Koipato, are described in the Paradise Range ("Ellsworth" Range; Spurr, 1903), at Quartz Mountain (U. S. Geol. Survey, 1927), in the Yerington district (Knopf, 1918), and at other localities in western Nevada and eastern California. These occurrences, together with those mentioned above, appear to delimit at least the minimum extent of this late-Paleozoic volcanic terrain.

A much greater extent, however, may be reasonably postulated. From the Baker quadrangle of northeastern Oregon Gilluly (1937) describes the Clover Creek greenstone as consisting of several thousand feet of "altered volcanic flows and pyroclastic rocks, with subordinate conglomerate, limestone, and chert." The associated sedimentaries have yielded a "Permian" fauna. Ross (1938) has mapped the Clover Creek formation eastward from the Baker region to within a few miles of the Snake River, from the canyon of which a limestone intercalated in similar greenstone carries fossils identified by Girty (Ross, 1938) as of Phosphoria age.

Although these volcanics may be in a large part of submarine origin, as suggested by Gilluly (1937), they nevertheless appear to indicate the geographic trend (northward from western Nevada) of this Anthracolithic volcanic activity; and if this be true, they likewise indicate the probable trend of a barrier between the Phosphoria and Pacific seas. It should be noted that the trend of this axis through northeastern Oregon, although slightly farther west, agrees closely with that proposed by Nolan (1928).

SYSTEMATIC DESCRIPTIONS

Class PISCES
Subclass ELASMOBRANCHII
Order SELACHII
Family EDESTIDAE
Genus HELICOPRION Karpinsky, 1899
Genotype, *H. bessonowi* Karpinsky, 1899.

HELICOPRION NEVADENSIS Wheeler, n. sp.

Text figure 3

Holotype.—University of Nevada, Mackay Museum Paleontological Coll., no. 1001, collected by Elbert A. Stewart in 1929. Plastotypes in the British Museum (Natural History), University of California, and Stanford University.

Description.—The single specimen upon which this species is based consists of an external mold showing the major part of very little more than 2½ volutions. The greatest diameter measures 120 mm. None of the coils are in contact, the relative amount of separation being unmeasurable because of a slight distortion of the specimen. The teeth, as best they can be estimated, number about 37 for the first volution, 39 for the second, and 19 for the first half of the third.

For the purpose of description, and in accordance with Karpinsky's description of the genotype, the teeth are regarded as consisting of three parts (fig. 2); first, the cutting blade, which lies between the apex and the points of contact with adjacent teeth; second, a middle part; and, third, a narrowed base inclined toward the older (smaller) teeth of the series. In the smaller teeth the blade is relatively the longest; while in the largest teeth each of the three parts consists of about one-third of the total length. At the end of the first volution, the blade forms about three-eighths of the total length; and

the line separating the other two divisions is not sharply defined at this stage. In the teeth of the first volution, the narrowed base extends forward to a point directly below the middle of the adjacent tooth; those of the largest teeth, however, extend to the middle of the second tooth in advance. As in most described specimens of *Helicoprion*, all teeth are apposed to one another symmetrically; i.e., the ends of the bases are

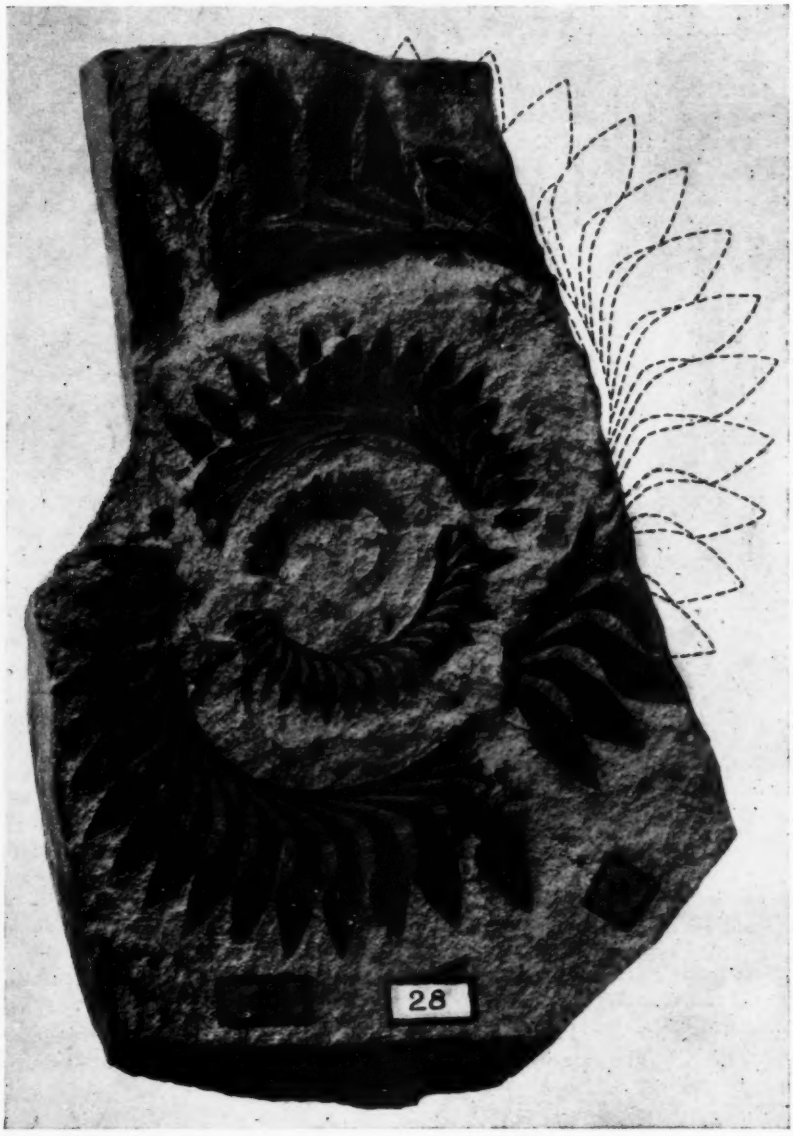

FIG. 3.—*Helicoprion nevadensis* Wheeler, n. sp., retouched holotype, ×1; University of Nevada, Mackay Museum Paleontological Coll., no. 1001; U.N. loc. 28, about 4000 feet below the top of the Rochester trachyte, Rochester district, Humboldt Range, Pershing county, Nevada.

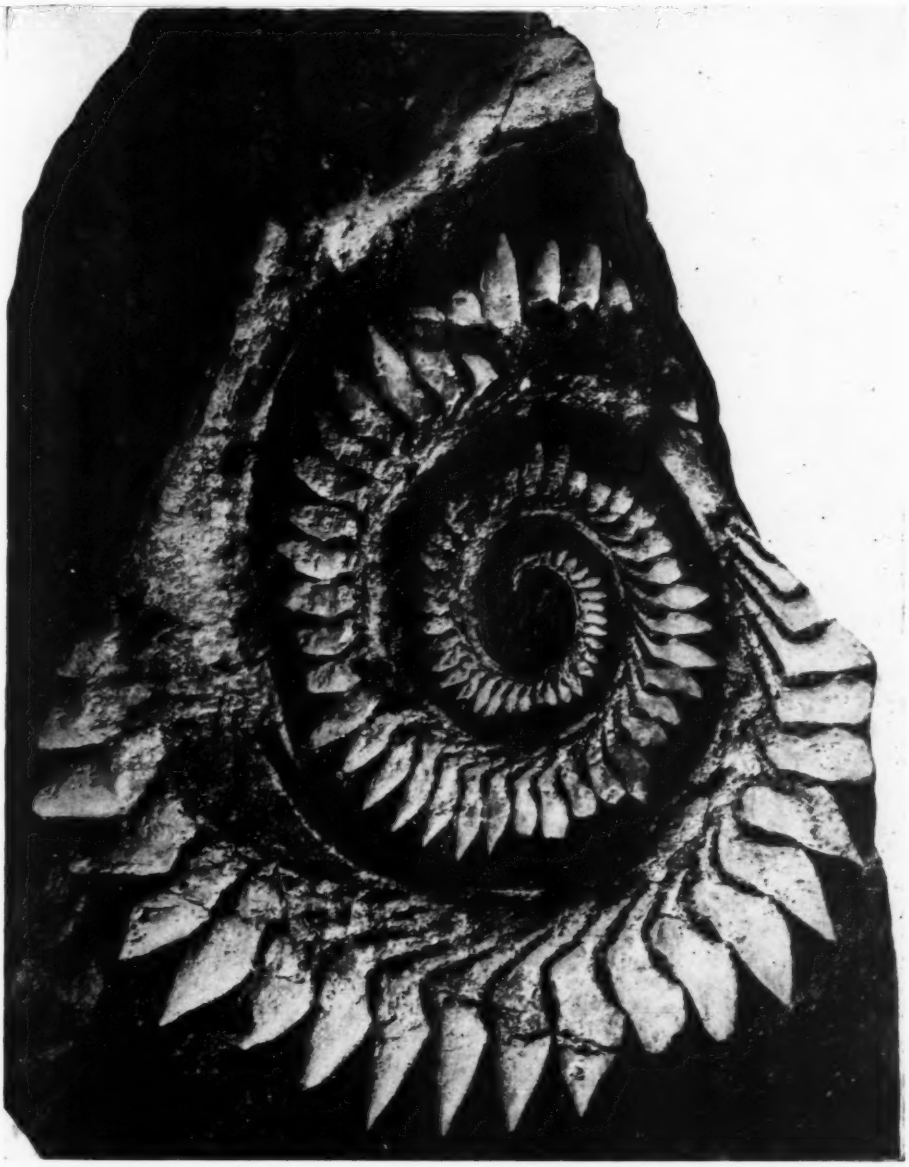

FIG. 4.—*Helicoprion sierrensis* Wheeler, n. sp., retouched holotype ×1; University of Nevada, Mackay Museum Paleontological Coll., no. 1002; U.N. loc. 29, glacial moraine on the southeast side of Frazier Creek, Downieville quadrangle, Plumas county, California.

not in lateral scalelike apposition to those of adjacent segments.

The teeth at the end of the first volution are 9.4 mm long, and their greatest width (at base of blade) is 2.7 mm. Those at the end of the second volution are 25.5 mm long and 6.5 mm wide. The largest complete tooth is 39 mm long and 9 mm wide.

The apical angle (measured between apex of cutting blade and points of contact with

adjacent teeth) is 42° at the end of the first volution, 37° at the 1½-volution stage, 43° at the end of the second, and 45° at 2½ whorls.

The edge of the cutting blade is finely serrate, the larger ones showing about 15 small denticles on each side of the apex.

The interdental spaces which separate the middle and narrowed portions of adjacent teeth are relatively wider in the earlier than in the later growth stages.

The width of the shaft at the base of the teeth is equal to about one-tenth of the volution height.

Comparisons and affinities.—Helicoprion nevadensis more closely resembles the genotype, *H. bessonowi* Karpinsky, than any other described species. The principle difference between these two is the relatively greater width of the shaft in *H. nevadensis*. In this respect, the Nevada species takes an intermediate position between *H. bessonowi* and *H. ferrieri* (Hay) from the Phosphoria formation of Idaho and Wyoming. In the genotype the shaft width is equal to about one-fifteenth of the volution height; in *H. nevadensis*, to one-tenth; and in *H. ferrieri*, to one-fifth.

One other noteworthy difference exists between *H. bessonowi* and *H. nevadensis*. The middle part of the teeth is defined at an earlier stage, and the relative length of this middle part increases more rapidly and to a greater extent in the Artinsk form than in the Rochester specimen. In the former, the middle portion greatly exceeds the length of the blade at the 2½-volution stage; while in the latter, the two divisions are about equal. In this feature, also, this new species must be regarded as constituting an intermediate stage between the genotype and *H. ferrieri*.

Preservation and matrix.—The fossil, an external mold, is impressed in a fine-grained tuffaceous shale. A petrographic examination by Gianella (1937) reveals that

> it consists of about 50 per cent quartz, with occasional feldspar fragments; and the remainder is mostly fine fragmental glass. There are also occasional muscovite fragments and minute grains of pyrite. Some fine-grained material appears to be carbonaceous. The largest quartz grain measures 0.18 mm; while the average lies between 0.01 and 0.05 mm. The quartz is very angular, none of it showing any appreciable rounding.

Type locality.—U. N. loc. 28, Rochester district, Lovelock quadrangle, Pershing County, Nevada. Map: U. S. Geol. Survey, Bull. 762, pl. 1. Lens of tuff exposed on the north slope of Sunflower Hill, about 100 feet west of the drain running northward from the saddle at B.M. 6671; also, about 100 feet west of a line between B.M. 6671 and B.M. 6237, at a point about 700 feet north of the former. Elevation: 6400 feet. SE ¼, SW¼, sec. 16, T. 28 N., R. 34 E.

Formation.—About 4000 feet below the top of the Rochester trachyte, as mapped by Knopf (1924). Anthracolithic (Uralian or Artinskian).

HELICOPRION SIERRENSIS Wheeler, n. sp.
Text figure 4

Holotype.—University of Nevada, Mackay Museum Paleontological Coll., no. 1002, collected by J. H. Menke of Blairsden, Calif., in 1931. Plastotypes in the British Museum (Natural History), University of California, and Stanford University.

Description.—The one specimen of this species known to date consists of an external mold to which adhere, in places, portions of silicified teeth and shaft. The specimen shows the greater part of 3¼ volutions, at which stage its greatest diameter is estimated to be about 170 mm. The whorls are not in contact, the amount of separation increasing gradually from about 1 mm in the first volution, to 8 mm at the largest stage represented. The teeth number about 32 in the first volution, 36 in the second, and about 41 in the third.

The cutting blade constitutes about half the entire length of the tooth at the end of the first whorl, where the middle part and narrowed base are not sharply defined; at the three-volution stage the cutting blade and middle part each constitute about 0.3, and the base about 0.4 of the entire length. The narrowed bases of the teeth of the first volution extend to a point below the middle of the projacent tooth; those of the third volution extend forward to the middle of the second tooth in advance. In this specimen, as in *H. nevadensis*, the teeth are apposed to one another in a symmetrical manner.

The teeth at the end of the first volution measure about 7 mm long and 2.4 mm wide; those at the end of the second, about 20

mm long and 5 mm wide; and those at the end of the third, about 40 mm long and 9.5 mm wide.

The apical angle appears not to change progressively with the size of the teeth, but varies irregularly between 34 and 37 degrees.

The interdental spaces are but little wider, relatively, in the early stages than in the later ones.

The shaft width equals about one-tenth of the volution height.

Comparisons and affinities.—*Helicoprion sierrensis* is rather similar to *H. nevadensis*. These two species are alike in the relative width of the shaft, and in the equality of length of the cutting blade and middle portion of the larger teeth. The California species differs from *H. nevadensis*, however, in its longer cutting blades of the early stages, its longer bases in the later ones, and its smaller apical angles.

Preservation and matrix.—Gianella (1937) has determined the rock in which this external mold is imbedded as a crystal tuff composed of about seventy per cent feldspar, equally proportioned between orthoclase and plagioclase; and about thirty per cent hornblende, approximately half of which has been replaced by epidote. Only an occasional feldspar grain is rounded; the others being cleavage fragments, with an occasional well-formed crystal. The plagioclase is predominantly medium oligoclase, although there are a few grains of acid andesine. The larger fragments of orhtoclase range from 0.4 mm to 0.8 mm, and those of plagioclase occasionally reach 1.04 mm in length. The largest hornblende fragment measures 0.57 mm.

Type locality.—U. N. Loc. 29, Downieville quadrangle, Plumas County, California. In a glacial moraine at a point about 5000 feet southwest of the Middle Fork of the Feather River, and 600 feet southeast of Frazier Creek. Elevation: about 4600 feet. SE ¼ of the SE ¼, sec. 22, T. 22 N., R. 12 E.

Formation.—Found in a glacially transported boulder in the valley of Frazier Creek, derived from either the "augitic greenstone series" or the Milton formation (more probably the former), of Anthracolithic (Uralian or Artinskian) age.

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SUCCESSION OF LATE CAMBRIAN FAUNAS IN THE NORTHERN HEMISPHERE

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ABSTRACT—The following Late Cambrian faunas are known in the Northern Hemisphere: The *Cedaria* in western Newfoundland and eastern Asia, the *Crepicephalus* in Newfoundland, and the *Aphelaspis*, of Dresbachian age; the *Elvinia* in Novaya Zemlya, Scandinavia, southeastern Newfoundland, and eastern Asia, the *Irvingella major* (with which is correlated the *Olenus* fauna), the Conaspid in eastern Asia (with which is correlated the *Peltura* faunas in Scandinavia, New Brunswick, and Nova Scotia), the *Ptychaspis*, the *Prosaukia* in eastern Asia, the *Briscoia* in the northern Appalachians and eastern Asia, and the lower *Dikelocephalus*, of Franconian age; the *Scaevogyra*, the upper *Dikelocephalus*, the *Eurekia* in eastern Asia, the *Saukiella* in the northern Appalachians and eastern Asia, and the *Plethopeltis*, of Trempealeauan age.

THE RECENT discovery of several diagnostic European trilobites in Upper Cambrian faunas from the Rocky Mountain region makes possible the first precise zonal correlation of Late Cambrian horizons of the Northern Hemisphere. This correlation has been effected in part by the discovery of definite evidence that the *Elvinia* fauna of the Franconia stage is the equivalent of the "*Agnostus*" *laevigatus* and *Agnostus pisiformis* faunas of the North Atlantic basin, as shown in fig. 1.

The Upper Cambrian faunal zones of Sweden, as arranged by Dr. Westergård (1922, p. 98), are the recognized Late Cambrian standard sequence for the North Atlantic basin, and are, reading from below upward:

"*Agnostus*" *laevigatus* zone: *Acrocephalites stenometopus, Leperditia, Lingula*
1. *Agnostus pisiformis* zone: *Acrocephalites stenometopus, Schmalenseeia, Proceratopyge*
2. *Olenus* zone: *Homagnostus obesus, Glyptagnostus reticulatus, Acrocephalites? rarus,* all species of *Olenus*

These initial zones are characterized by small assemblages of well defined genera and species which are strictly limited to these horizons (with the exception of a species of *Proceratopyge* and *Homagnostus obesus*, which occur at the base of zone 3). The following four horizons, though individually characterized by one or two distinct genera, are unified by the continued presence of species of *Parabolina*.

3. Zone of *Parabolina spinulosa* and *Orusia lenticularis:* appearance of *Parabolina, Pseudagnostus cyclopyge, Protopeltura,* and *Conokephalina*
4. Zone of *Leptoplastus* and *Eurycare: Leptoplastus, Eurycare, Protopeltura,* and *Parabolina spinulosa*
5. Zone of *Peltura, Sphaerophthalmus,* and *Ctenopyge:* (four subzones), *Peltura, Sphaerophthalmus, Ctenopyge, Parabolinella, Parabolina, Megalaspis, Lotagnostus trisectus,* and "*Agnostus*" *rudis*
6. Zone of *Acerocare, Cyclognathus,* and *Parabolina: Acerocare, Cyclognathus, Parabolina, Niobe,* and *Megalaspis*

In a collection from Dinwoody Canyon, Wyoming, a species of *Acrocephalites* is associated with a typical *Elvinia* fauna, consisting of species of *Camaraspis, Elvinia* and *Pterocephalia*. More recently another species of *Acrocephalites* has been recognized in the *Irvingella major* zone of the Upper Cambrian section of Wisconsin.

It should be understood that the genus *Acrocephalites* is here used in the strict sense. Many North American species have been referred at various times to this genus, but Resser has shown (1935, p. 2) that none of these species is in any way related to the European *Acrocephalites*. The new species

of this genus from Wyoming and Wisconsin are therefore the first known representatives of true *Acrocephalites* to be discovered in North America.

In Europe only three species of this genus are known:—*A. stenometopus* (Wallerius), the genotype, from the "*Agnostus*" *laevigatus* and *Agnostus pisiformis* zones of Scandinavia; *Acrocephalites? rarus* Westergård from the *Olenus* zone of Scandinavia; and *A. vigilans* Walcott and Resser from strata in Novaya Zemlya. *Acrocephalina* (a genus related to *Acrocephalites*) and *Irvingella?* occur, together with *Lotagnostus asiaticus*, in Upper Cambrian beds in the eastern T'ien-shan, according to Troedsson (1937, pp. 12–13).

The fauna from Novaya Zemlya associated with *A. vigilans* was considered Lowre Ozarkian in age at the time it was described by Walcott and Resser (1924, p. 1). However, it contains, besides *Acrocephalites* and *Agnostus pisiformis*, a species of *Irvingella* very close to *I. major*, and the genus *Pesaia*, which is closely related to, if not identical with, *Elvinia*. The presence of the first two trilobites mentioned indicates that this fauna is the approximate equivalent of the *Agnostus pisiformis* zone of Sweden, while the two latter permit a close correlation of the fauna with that of the Ironton horizon of North America.

Thus it appears that *Acrocephalites* has a wide geographic distribution but a very short stratigraphic range, being confined to strata of Ironton age. On this evidence the

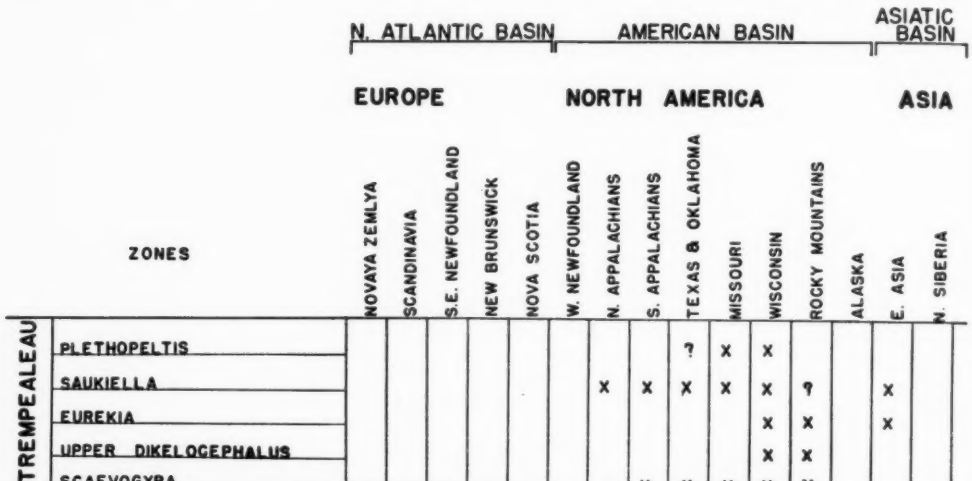

FIG. 1.—Late Cambrian faunal sequence in the northern hemisphere.

Elvinia fauna of the United States is considered to be directly correlatable with the "*Agnostus*" *laevigatus* and *Agnostus pisiformis* faunas of Scandinavia.

In southeastern Newfoundland and New Brunswick have been found faunas of the Atlantic province, which are also apparently of the same age as the two above mentioned zones.

A similar close correlation between the succeeding faunal zones of the Franconia of this country and the Olenid beds of the North Atlantic region can not be made at present, but during recent work on Upper Cambrian faunas new information has been secured which adds to the knowledge of the relationships of the faunas of these zones. In a small collection said to have come from Quinn Canyon Range, Nevada, several excellently preserved specimens of an agnostian very similar to *Homagnostus obesus* (Belt) were discovered. The associated fauna consists of *Acrotreta microscopica* (Shumard), a new species of *Elvinia*, and *Pterocephalia*[1] *occidens* (Walcott), all species of the *Elvinia* and *Irvingella major* faunas of the United States. The presence of a *Homagnostus* very close to *H. obesus* may be regarded as marking the Nevada assemblage as approximately the equivalent in age of the *Olenus* zone. An *Elvinia* fauna, also containing a species of *Homagnostus*, has been found by J. F. Mason in the Desert Range of Nevada. The faunal and stratigraphic evidence obtained to date suggests that the *Olenus* zone is equivalent in part, at least, to the *Elvinia* and *Irvingella major* zones and may, in part, be either contemporaneous with the base of the Conaspid zone[2] or else with a faunal hiatus immediately preceding that zone. *Irvingella* has been reported by C. J. Stubblefield (1932, p. 65) from England, where it occurs in an exposure not far from an outcrop of shales containing *Olenus;* but it has not been determined whether the *Olenus* shales are older than those holding *Irvingella*, or younger.

The occurrence in the Conaspid fauna of a genus which closely resembles *Parabolinella*, characteristic of subzone *b* of the *Peltura* beds of Scandinavia, suggests the approximate equivalence in age of the Conaspid and *Peltura* faunas. The earlier species of Raasch's unpublished genus "*Maustonia*" show a marked resemblance to *Parabolinella* and also to the more common related genus, *Parabolina*. The discovery in the *Ptychaspis-Prosaukia* faunas of Wyoming of a species of agnostian belonging to the same genus as "*Agnostus*" *rudus holmi*, which occurs in the upper beds of zone 5 in Sweden, suggests that in all probability the highest beds of the zones characterized by *Parabolina* and *Peltura* may be as young as the *Ptychaspis-Prosaukia* beds of the Franconia.

The faunal sequence for the Northern Hemisphere, in the light of present knowledge, is shown in figure 1. This sequence has been compiled from all the published and much of the unpublished data that is available. The Scandinavian section is that published in Westergård's (1922, p. 98) monograph on the Upper Cambrian Olenid faunas. The Asiatic section is from recent publications by Sun (1935, p. 7) and Kobayashi (1933, p. 80). Although their sections agree in all essential details, the nomenclature for the faunal zones employed by the Japanese and Chinese geologists is frequently different. The nomenclature adopted in this paper is the one proposed by Dr. Sun.

The *Cedaria* fauna, generally recognized as the oldest Late Cambrian fauna, is now known from western Newfoundland to the Rockies. In the southern Appalachian and Interior provinces this fauna is characterized by the genus *Cedaria* throughout the zone; but in western Newfoundland and the Rocky Mountain province *Cedaria* is rarer in occurrence and apparently restricted to the basal beds, and the dominant genus of

[1] Several species of this genus (incorrectly spelt *Pterocephalus*) were described from China by Walcott. However, only *P. asiatica*, of which the cranidium is known, was regarded by Kobayashi as valid (1935a, p. 231). It was later placed in *Paracoosia* by Kobayashi (1936b, p. 172); but is regarded as a valid species of *Pterocephalia* by Bridge (1937, p. 250). *P. bursiris*, known only from the pygidium, may be a *Prosaukia*. Dr. Sun has recently obtained two more pygidia which he has referred to this species from the Licheng formation near Licheng, Shansi. These specimens are associated with *Ptychaspis*, *Prosaukia* and *Tsinania*.

[2] The Conaspid zone is characterized by species of "*Maustonia*," *Stigmacephalus*, *Orygmaspis*, *Taenicephalus* and *Conaspis*.

the faunal assemblage is *Arapahoia*. Of the two succeeding faunas, the *Crepicephalus* fauna is known from western Newfoundland to the Rockies; and the *Aphelaspis* fauna has been found from the central Appalachian region (Tennessee) to the Rockies with the exception of the Missouri area, where over 300 feet of unfossiliferous Bonneterre dolomite intervene between the *Cedaria* zone and the *Elvinia* zone of the Davis formation. Though distinctive in their individual assemblages, these three faunas have one or more genera common to all of them and constitute a well defined group that is sharply separated from the succeeding faunas. The lower two are more closely related to each other than to the *Aphelaspis* fauna. No evidence of faunas of this age (Eau Claire) has ever been found in the North Atlantic region east of western Newfoundland. The oldest Late Cambrian faunas of southeastern Newfoundland and northwestern Europe are the "*Agnostus*" *laevigatus* and *Agnostus pisiformis* faunas, which are now believed to have been contemporaneous with the *Elvinia* fauna.

The widely distributed *Chuangia* fauna of Asia is considered to be the approximate equivalent of the *Cedaria* fauna. This correlation is based upon the presence in the faunas of this age from Missouri and Montana of the genus *Genevievella*, the latter of which is closely related to *Chuangia*, differing from it only in the length and shape of the posterolateral limbs of the cranidium.

The next younger faunal zone of China recognized by Sun, the *Changshania* zone, is also probably Eau Claire in age; but an exact zonal correlation with it is not possible at present, as the only evidence available is its stratigraphic position and the presence in it of a species belonging to a new agnostian genus, which is the characteristic agnostian genus of all three of the Eau Claire faunas.

For the lowermost faunal zone of the Franconia, the *Elvinia* zone, a precise correlation throughout the Northern Hemisphere is possible. As has been previously mentioned, the *Elvinia* zone of the United States is the direct equivalent of the lowest Upper Cambrian zones in the Scandinavian region and of the zone in Novaya Zemlya[3] characterized by *Irvingella* and *Pesaia* (=*Elvinia?*). In this fauna there also occurs the genus *Koldinia*, which characterizes a fauna from northern Siberia now being described by Howell and Kobayashi. Thus these four widely separated faunas are all directly correlatable.

The exact stratigraphic position of the *Kaolishania* fauna, which succeeds the *Changshania* fauna in eastern Asia, is not yet definitely determinable. Such evidence as is now available—(1) the appearance of *Pseudagnostus* in the form of *P. cyclopygeformis* and a species identified by Sun as *P. cyclopyge*, (2) the presence of *Conokephalina*, and (3) the preponderance of genera of the Ceratopygidae—indicates that this fauna is of early Franconian age. It may be in part as old as the Ironton, for in North America *Pseudagnostus* occurs in the *Elvinia* fauna, and in Sweden *Proceratopyge* is present in the *Agnostus pisiformis* zone. However, the presence in the *Kaolishania* fauna of *Conokephalina* and "*Pseudagnostus cyclopyge*," a genus and a species diagnostic of the *Parabolina spinulosa* zone of the North Atlantic region, would seem to indicate that the *Kaolishania* fauna is more nearly the equivalent of the *Parabolina* faunas of Europe and the *Conaspis* faunas of the United States. *Elkia*, described by Walcott from the Eureka district, Nevada, has been reported from the *Kaolishania* fauna by Sun. Unfortunately, the exact stratigraphic position of *Elkia nasuta* (Walcott), the genotype, in the United States section is unknown, but species tentatively identified as *Elkia* have been reported from the base of the Signal Mountain formation by Ulrich (1932, p. 746).

Two small fragmentary collections originally described as containing the genus *Olenus* have been reported from widely separated localities in the United States and western Canada. At Cedar Bluff, Alabama, specimens were collected by C. Butts from shales and interbedded limestone nod-

[3] A careful examination of all the described species and of the account of localities given by Holtedahl (1922, p. 343) brings out the fact that apparently faunas equivalent not only to the *Elvinia*, but also to the Conaspid and *Ptychaspis-Prosaukia* zones of the Franconia, are to be found in this region.

ules assigned to the upper Conasauga formation and were identified by him (1926, p. 76) as "*Pseudagnostus*" *reticulatus* and "*Olenus* cf. *O. truncatus*." The former is a species very similar to *Glyptagnostus reticulatus* (Angelin), and the latter has been assigned to the new genus and species *Proaulocopheura buttsi* by Kobayashi (1936a, p. 93), who considered the genus to have no relationship with the Olenidae. In this connection it should be mentioned that the genus shows a marked resemblance to *Aphelaspis;* and that extensive field work will be undertaken as soon as possible to secure a better and larger collection from this locality and to determine the stratigraphic relationship between these beds and the strata carrying the *Cedaria* fauna at the famous locality on Coosa River. At present, the occurrence of the *Glyptagnostus* is the only evidence available for correlating this fauna with that of the *Olenus* zone. *Glyptagnostus reticulatus* occurs in the Olenus fauna of northwestern Europe. The genus *Glyptagnostus* has been found also on the Alaska-Yukon border (its faunal associations there are not known to the authors) and has been reported by Whitehouse (1936, p. 77) from Queensland, where it is said to be associated with *Pseudagnostus*, *Olenus*, and *Proceratopyge*.

From an unnamed formation north of Jubilee Mountain, British Columbia, C. S. Evans obtained a small fauna (1933, p. 125A II) stated by Resser to contain *Olenus*, *Housia?*, *Pseudagnostus* sp., *Glyptagnostus reticulatus*, and *Agnostus pisiformis*. The specimen assigned to *Olenus* has since been restudied by Kobayashi (1936, p. 92) and described as *Parabolinella? evansi*. As the identification of the second specimen as *Housia* is questioned by Resser, and as the agnostian *Pseudagnostus* occurs throughout the Franconia stage, it is at present impossible to give a zonal correlation for this collection, but the presence of *Glyptagnostus* and *Agnostus* of the *pisiformis* type suggests a basal Franconia age (*Elvinia* zone).

Kobayashi's restudy of these two collections indicates that the genus *Olenus* has never yet been found in North America west of New Brunswick; and the present status of Late Cambrian faunal knowledge definitely suggests that the only regions in this basin in which genera of the Olenidae might be found are the Canadian Rockies and Alaska, where the Late Cambrian formations have never been carefully studied.

In New Brunswick and southeastern Newfoundland are *Olenus* faunas very similar to those of Europe.

The Conaspid zone is considered to be the equivalent of the *Parabolina*, the *Leptoplastus*, and a part of the *Peltura* zones of the North Atlantic region. The evidence for this correlation is (1) the marked resemblance between "*Maustonia*" and *Parabolinella* and *Parabolina;* and (2) the occurrence of the faunas at similar stratigraphic positions above a horizon which has been accurately correlated (the *Elvinia* zone), as has been previously discussed. The reasons for believing that the uppermost zones of the Olenid beds are at least as young as the *Ptychaspis-Prosaukia* faunas of America have also been mentioned (p. 117).

The *Ptychaspis-Prosaukia* fauna, which overlies the Conaspid fauna, can be divided into three subfaunas: (1) a lower zone, characterized by *Ptychaspis granulosa* (Owen) and allied species; (2) a middle zone, marked by *Ptychaspis miniscaensis* (Owen) and allied species and the first appearance of species of *Idahoia* and *Prosaukia;* and (3) an upper zone in which *Briscoia* is dominant. The entire fauna is apparently absent from the Missouri and southern Appalachian region but occurs in Texas and Oklahoma. *Idahoia calcifera* (Walcott) and *Saukia speciosa* (Walcott), described from the Hoyt formation of New York, probably represent the *Briscoia* zone. In the Rocky Mountain region faunas of all three zones are present, but that of the *Prosaukia* zone is the best developed and most widespread. The beds in the Ovid formation of Utah which carry *Idahoia serapio* Walcott and *I. maladensis* Walcott probably belong to the *Prosaukia* zone. Faunas of the *Briscoia* zone have been described by Kobayashi (1935 b, pp. 39–68) from Hard Luck Creek, Alaska, and from the Phillipsburg quadrangle, Montana, and by Meyerhoff and Lochman (1935, p. 352) from the Black Hills, South Dakota.

Throughout eastern Asia occurs a fauna (the *Ptychaspis subglobosa* zone of Sun) which is characterized by an abundance of

species of *Prosaukia* and *Ptychaspis*, and which can be directly correlated with the *Ptychaspis-Prosaukia* fauna of the United States. The prominence of *Prosaukia* in the Asiatic fauna indicates an equivalence of this fauna with the two upper zones in this country; and the presence of a species of *Calvinella* suggests that the upper portion of the *Ptychaspis subglobosa* zone may be as young as the Lower *Dikelocephalus* zone of America.

The uppermost fauna of the Franconia, the lower *Dikelocephalus* fauna, is characterized by the appearance of *Dikelocephalus*, *Illaenurus*, *Saukiella*, and *Maladia*. It has been definitely recognized only in Wisconsin and at a few localities in the Rockies.

The faunas of the Trempealeau stage, comprising the youngest Late Cambrian strata in this country, are here grouped into two divisions for simplification. The oldest of these faunas, characterized by the appearance of *Scaevogyra*, is a unit which can be distinguished throughout the Appalachians and the Mississippi Valley, but is apparently rare in the Rocky Mountain region.[4] In Wisconsin four younger faunas—the upper *Dikelocephalus*, the *Eurekia*, the *Saukiella*, and the *Plethopeltis*—have been recognized. Faunas correlatable with these upper zones occur in the Appalachians, Missouri, Texas and Oklahoma, and at a number of widely scattered localities throughout the Rockies; but unless genera and species diagnostic of the particular fauna in Wisconsin have been found, no exact zonal correlation is possible. At present the only faunas that can be accurately correlated are (1) those of Texas and Oklahoma, which belong to the *Eurekia* and *Saukiella* zones; (2) a Trempealeau fauna of Montana and Wyoming, which is of *Eurekia* age; (3) a fauna from New Mexico, which is apparently of upper *Dikelocephalus* age; and (4) a fauna from Nevada, which is of *Eurekia* age.

In Asia, Sun's very widely distributed *Quadricephalus walcotti-Saukia acamus* fauna is the equivalent of Trempealeau faunas of this country; but at the present time more detailed zonal correlations between the two regions can not be made.

The great prominence of primitive graptolites in the Trempealeau faunas, a feature that has long been known in the Wisconsin section but the importance of which is being reemphasized by the discovery of abundant and widespread graptolite remains in beds of this age throughout Montana and Wyoming, suggests the possible contemporaneity of the Trempealeau faunas of America with at least a part (probably the lower part) of the Tremadocian faunas of the North Atlantic basin. Additional evidence for this opinion is the occurrence in the fauna of the Gorge formation of Vermont (of Trempealeau age) of a few trilobite genera that appear to be related to genera in the *Ceratopyge* fauna (Raymond, 1937, pp. 1132–1133).

It is interesting to note in connection with the faunal sequence just discussed that the oldest known Upper Cambrian strata of New Brunswick, Nova Scotia, southeastern Newfoundland, and Europe were deposited, according to the correlation here proposed, after an important land movement that affected all parts of the United States as well as the North Atlantic basin. The greatest faunal hiatus in the Upper Cambrian section of the United States is the one between the *Aphelaspis* and the *Elvinia* faunas. In the majority of the regions of this country studied to date, this horizon is marked by sharp lithologic changes indicative of a widespread epirogenic movement, which resulted in the elevation of thousands of square miles of sea bottom, so that wide areas were either drained completely or left covered only by shallow water. This is the case in the Appalachians, Nevada, California, the Mississippi Valley, Texas, the Black Hills, Wyoming, and Montana. The reestablishment of marine conditions in these areas at the beginning of Franconian time was caused by a new encroachment of the Late Cambrian seas.

A brief summary of the sedimentary evidence of this hiatus will be of interest here. In Wisconsin the Galesville sandstone is apparently of fresh water origin. The Ironton sandstone of the Franconian stage begins with a basal conglomerate and coarse sandstone; and a marked difference, both

[4] A specimen from the Chokecherry dolomite (Lower Ordovician) has been identified by E. Kirk as *Scaevogyra?* sp. (Nolan, 1935, p. 15).

in percentage and kind, in the heavy mineral content has been found to occur between the Galesville and the Ironton (Wanenmacher, Twenhofel and Raasch, 1934, p. 11). In Missouri there is a sharp lithologic change at the boundary between the Bonneterre dolomite and the basal beds of the Davis shale carrying the *Elvinia* fauna. This sudden change from dolomite to shale indicates decided uplift throughout the southeastern Missouri area. In Texas the Lion Mountain sandstone member at the top of the Cap Mountain formation represents the sedimentation conditions at the close of Dresbach time. All evidences of marine life are lacking above the basal two feet of the member. In the Appalachians a lithologic change occurs at the boundary between the Nolichucky shale and the overlying Copper Ridge dolomite. This condition may represent either a local deepening of the sea in this region or else a change in the conditions of sedimentation, which resulted in the deposition of dolomite and thin shales rather than limestone and shale, which characterize the Nolichucky. The section of the Upper Cambrian strata on the west side of Clinch Mountain, Tennessee (Hall and Amick, 1934, p. 167), suggests such an occurrence. In the Black Hills there is a noticeable lithologic difference between the pure limestone of the *Aphelaspis* zone and the thin-bedded gray-green shales of the *Elvinia* zone, a change considered to be indicative of a shallowing of the basin and an uplift of the adjacent land areas. In Montana there is an abrupt change from pure limestones at the top of the Maurice to sandstones or green shales at the base of the Snowy Range. This is also true of Nevada and California, where the *Elvinia* green shales seem to transgress the lower dolomites.[5] In Wyoming, however, a sharp lithologic change at this horizon apparently exists only in sections in the eastern part of the state.

Thus the occurrence of an important land movement between the Dresbach and Franconia stages is definitely confirmed by both faunal and lithologic evidence throughout the greater part of the United States; and, according to the Late Cambrian correlation here proposed, this stratigraphic break was of profound significance in all portions of the Northern Hemisphere.

[5] Mason, J. F., personal communication.

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SUGGESTIONS REGARDING THE TAXONOMY AND NOMENCLATURE OF CRETACEOUS AND TERTIARY PLANTS

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ABSTRACT—The ascription of fossil leaves to modern genera on insufficient evidence has created confusion and uncertainty in paleobotanical taxonomy and nomenclature. Failure to take into account variation within the species has caused redundency of names. The ecological approach is helpful and should not be neglected. A thorough revision of fossil dicotyledon floras and floral lists appears long overdue.

THE STUDY of the fossil dicotyledons has been rendered needlessly difficult by the lack of care in the generic determination of fossil leaves and by the indiscriminate multiplication of species. The reference of leaves of fossil dicotyledons to modern genera is an accepted practice with paleobotanists, but one which, in the writer's opinion, should be discontinued. In many cases taxonomists find it impossible, upon leaf characters alone, to place even a modern plant in its correct genus. Generic determination becomes even more difficult when one must deal with the frequently imperfect impressions of fossil leaves. Again, it is by no means improbable that some of the fossil plants were generalized ancestral types, which have subsequently evolved and differentiated into the modern genera. The difficulties of generic determination may in part be due to this possibility. One can only conclude that the reference, on insufficient evidence, of palaeobotanical specimens to modern genera leads to confusion.

Furthermore, the difficulties of nomenclature have been greatly increased by the indiscriminate multiplication and splitting of species which has been indulged in by certain workers, notably Ward and Hollick. It would appear that neither of these men took into account the variability of the leaves that grow upon a single tree. In some of their reports as many as a dozen or more species of a single genus are described from the same formation and locality. It is not usual, at least in the higher latitudes, to find more than two or three species of a single genus of woody plant growing in the same locality. If the fossil leaves of the dozen or more species are examined, it is obvious that they fall into fewer principal types, whose leaves do not vary more among themselves than do the leaves of a single tree of a living species. Obviously,

such a multiplication of fossil species is not only useless, but confusing.

The nomenclature of fossil dicotyledons has become so involved that palaeobotanists have found it necessary to cite long lists of synonymy in discussions of fossil species. Seward (1) in discussing the genus *Platanophyllum* Fontaine points out that leaves of the same morphological character have been ascribed to *Platanus*, *Aralia*, *Liquidambar*, *Sassafras*, *Sterculia*, *Cissites*, and to other genera. In the same paper he lists 11 species as synonyms of *Platanus latiloba* Newberry and says that they are either identical with *P. latiloba* or at least not to be distinguished from it by any well-defined or constant features. In a description of the Ravenscrag and Whitemud floras Berry (2) describes over a dozen species whose synonymies contain four or more names. Many similar examples could be cited. The need for revision and simplification is obvious.

It is difficult to agree with the occasional practice of erecting a new specific name for a leaf that agrees in form and venation with one previously described but differs appreciably in age. The reason advanced is that the difference in age makes it improbable that the two leaves represent the same species. Botanically the plants upon which these leaves grew may or may not belong to the same species, but unless there are determinative features to separate them, there is no advantage in manufacturing and maintaining new specific designations. Such a practice only serves to obscure the relationships of one flora to another and to add to the complexity of the literature. If, later, differences are discovered that warrant a separation into two or more species, the erecting of new species should be done at that time. If it is necessary meanwhile to refer to the leaves from either formation separately, this could be done by mentioning the formation as well as the specific name.

Palaeobotanical lists show marked ecological discordances. For instance, cool temperate and boreal types such as *Populus*, *Betula* and *Alnus* are recorded from the same formation as such warm temperate and subtropical genera as *Ficus* and *Magnolia*. Such an association is highly improbable, and the most logical conclusion is that many of the plants have been incorrectly identified.

Broadly speaking, each of the major climatic divisions, Tropic, Temperate, and Arctic, has its own characteristic fauna and flora. Within these major divisions are subdivisions. On the American continent north of the Gulf of Mexico are three life regions (3), the Tropic, the Austral, and the Boreal, each subdivided into life zones characterized by its own peculiar assemblages of plants and animals. The Austral region is divided into the lower Austral, upper Austral, and transition zones, and the Boreal into Canadian, Hudsonian and Arctic zones. As an illustration of what is meant by a life zone, the upper Austral zone includes the hard wood forests of the east, the plains to the west and the lower lands of the Cordilleran region south of the 49th parallel; and the Canadian zone covers all the northern coniferous forests.

Quite obviously, there is a natural gradation from one life zone into the next, but in the main each zone is characterized by the presence of certain species and the absence of others. Therefore, when types characteristic of widely separated life zones are grouped in a floral list, the correctness of the identification of some of the species is to be questioned.

Potbury (4) has pointed out that very close agreement between the floral associations of the fossil floras and those of the present is not to be expected.

> The element of time, involving change in physical conditions alters floral associations and their component species so extensively that it is impossible to find an exact replica of a fossil flora among modern forests. The fossil assemblage becomes segregated, some species remaining as relicts, others migrating, still others becoming extinct. The original species, except those which have become exterminated, may evolve and give rise to one or more modern species, some retaining characters of the ancestral form, others acquiring new ones. A discussion of the habitat and distribution of living equivalents should, therefore, be restricted to those fossil species whose modern affinities are certainly established.

With this view the writer is in full accord, but he would point out that the apparent disparities betweens past and present floral associations may be due in part to incorrect

identification of constituent elements in the past floras.

The living floras of the world fall naturally into four major divisions or realms, as follows:

(1) The Boreal realm, including everything north of the Tropic of Cancer; (2) the Neotropic realm, including South America; (3) thePaleaotropic realm, including Africa, Southern Asia, and Australasia; (4) the Antarctic realm, including Antarctica, the southern tip of South America, and the mountain tops of southern Australia and Tasmania.

The floras of the Arctic and Subarctic regions of the New World are very similar in composition to that of the corresponding regions of the Old World. Most of the genera and many of the species are the same in these two areas. The farther south one proceeds, the more unlike the floras of the two hemispheres become, this unlikeness reaching a maximum in the mid latitudes of the southern hemisphere. As the Antarctic is approached there is a recurrence of boreal forms, and the floras become alike rather abruptly. These differences in the floras doubtless reflect the geologic separation of the lands of the two hemispheres. The absence of free routes of migration for the plants of the Southern Hemisphere has permitted a long period of separate evolution and consequent divergence of the palaeotropic and neotropic floras. In the northern lands free intermigration between the two hemispheres was possible over long periods of time, and even today, in the Arctic regions, the two areas are separated only by the narrow Behring Strait. Consequently, in a consideration of North American fossil floras, especially the more recent ones, the modern equivalents should be looked for among the plants of the Boreal and Neotropic realms rather than with those of the Palaeotropic region, with which there has obviously been a less close connection.

The great amount of inaccuracy and confusion in regard to generic identity, and the redundancy of species has taken away much of the value from our floral lists of fossil dicotyledons. It makes the identification of fossil leaves difficult and a comparison of floras well nigh impossible. Much of the published information regarding the geographic and temporal distribution of the various plant groups in past ages is unquestionably incorrect, and many evolutionary trends have been obscured by these same faulty records.

It is obvious that a revision of the Late Cretaceous and Tertiary floras is long overdue. It was the writer's intention to commence such a revision with a paper on the North American species of the genus *Trochodendroides*. Unfortunately, circumstances have arisen to postpone the completion of this research. Among other groups of fossil plants much in need of revision are the so-called genera *Platanus*, *Aralia*, *Ficus*, and *Viburnum*. For the purpose of minimizing the confusion now present and to prevent further complications in the future, it is suggested that revisers of floras and the describers of new ones should adopt the following recommendations:

1. The International Rules of Botanical Nomenclature should be followed.

2. The names of living genera should be used only for those fossils definitely referable to them on the basis of determinative fructifications.

3. Form genera should be used for all leaves that are not accompanied by such fructifications. Generic designations with endings like *opsis*, *oides*, or *phyllum* might be used to show possible or probable relationships to modern genera; for instance *Platanophyllum* for leaves probably belonging to *Platanus*. Leaves from the same locality and horizon as those accompanied by fructifications should be referred to the modern genus, but similar leaves coming from another region or horizon should be referred to the form genus, for generic identity cannot be certain. An exception to this rule might be made in the case of Pleistocene fossils, because the time elapsed has been so short that the plants probably belong to living species, which can usually be determined with a fair degree of accuracy by the ecological groupings. In the case of older floras whose constituent species have had sufficient time to evolve, such a procedure could not be followed with the same degree of certainty. By this usage living genera would be freed of all fossil plants not strictly referable to them, and the geo-

logical history and the past geographic distribution would become more apparent.

4. The natural variation of the leaves of a single species should be taken into account, and unnecessary duplication of species avoided.

5. Leaves of the same character and venation should be referred to the same form species even if the actual specific identity of the plants upon which they grew is rendered doubtful on account of difference in age.

6. The flora should be considered as a whole with regard to the ecological concordance of its constituents when pointing out probable relationships of the fossil species. In a study of the Cordilleran floras, Chaney and his associates have applied the ecological approach with considerable success.

In view of the present unwieldy and frequently inaccurate palaeobotanical floral lists and the confused state of their taxonomy and nomenclature, a thorough revision and simplification would be of inestimable value. Identification of fossil plants would then be easier, comparisons of floras facilitated, and floral assemblages would be of considerable value for the study of climatic zoning. It is quite conceivable that with the separation of plants definitely referable to modern genera from those fossils that can not be placed with certainty, new light might be shed upon the evolution of the dicotyledons. Finally, definite reliable information, now almost completely lacking, would be available regarding the past geographic distribution of various genera.

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STRUCTURE OF THE VERTEBRAL COLUMN IN EUSTHENOPTERON FOORDI WHITEAVES

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ABSTRACT—X-ray photographs of part of the vertebral column of *Eusthenopteron foordi* Whiteaves show that each vertebral segment consists of (1) a centrum made up of two thin lateral concentric half rings; (2) large paired neural arches and neural spines; and (3) small paired pleurocentra at the bases of the neural arches. There is no indication of more than one ring centrum associated with a neural arch, the intercentral space presumably having been cartilaginous. The embolomerous condition of early amphibians may have arisen through ossification of the cartilaginous intercentral space or by down growth of the pleurocentra to form a second ring, or by a combination of these two processes.

IT IS A surprising fact that, while Gadow and many other authors have studied the problem of the origin of vertebrae from embryological material in recent amphibians and reptiles, not much attention has been paid to the structure of the vertebrae of Palaeozoic crossopterygians. Although it is generally assumed that the embolomerous type of vertebrae found in primitive amphibians was derived from some crossopterygian ancestor, there is remarkably little direct evidence as to whether this two-ringed condition was present before amphibians arose.

In Woodward's "Catalogue of the fossil fishes in the British Museum" there are repeated statements indicating that he and all the authors summarized by him found ringlike centra in the Palaeozoic crossopterygians. Our material representing the genera *Eusthenopteron* (figs. 3 and 4), *Megalichthys* (fig. 1 A) and *Strepsodus* (fig. 1 B) fully confirms this statement. The rings, we may presume, were formed by ossifications outside of the elastic membrane which bounds the fibrous sheath of the notochord. These rings may not always be complete and the size of the lumen for the notochord may vary from very large in *Eusthenopteron* to fairly small in *Strepsodus*. In Bryant's *Eusthenopteron* he describes them as follows (1): "I find that the vertebral centra . . . are not, as has been supposed, ossified into complete rings. . . . Each centrum is made up of two lateral pieces which are not in contact with each other either above or below. . . . [Each one-half centrum] is thickest above and tapers ventrally."

The question arises, are these successive ring centra closely opposed to each other or are they separated by intercalated elements? Hussakof (4), in describing the beautifully preserved, large *Eusthenopteron* skeleton in the Albany Museum, says: "The centra are separated from one another by narrow spaces which increase backward until, near the end of the series, they are equal to the width of the vertebrae." In a specimen of *Megalichthys nitidus* (Cope's type of *Ectosteorhachis nitidus*) the four vertebrae immediately behind the skull are represented by the ventral halves of the rings (fig. 2 A). These are all closely appressed and are correctly figured by Hussakof (3). The intercentral spaces could not have been large. Again, in an isolated piece of this specimen which may come from the midcaudal region, there are four rings associated with five neural arches (fig. 2 B). Here there may have been room for intervertebral spaces, but the evidence is not decisive. At any rate there is no evidence of ossified intervertebral rings or of rings not attached to neural or haemal arches.

So far as we know, Watson and Day (6) are the only authors who have actually noted a two-ringed condition in a crossopterygian. According to them, "the vertebral

[1] Now at University of New Hampshire, Durham, N.H.

column of *Glyptolepis* is of a temnospondylous nature" with an "apparently rhachitomous" arrangement of the elements at the anterior end and a "nearly embolomerous" arrangement of the elements posteriorly. "In both regions the ossifications appear to be paired and are slender segments of rings." They further state that "this specimen is of considerable importance because it is the only fragment of a Palaeozoic fish showing a vertebral column of this type, and it is certain that the Amphibia arose from fish with a temnospondylous vertebral column of some form."

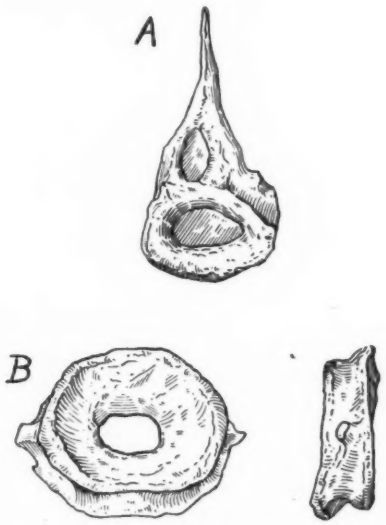

FIG. 1.—Vertebrae of A, *Megalichthys;* B, *Strepsodus.*

Noble (5), in his discussion of vertebrae says, "The vertebrae of some modern fish, such as *Amia*, are embolomerous in part, in that a single neural arch is associated with two centra in each segment. The same was true of some of the vertebrae of the crossopterygian fish *Eusthenopteron*, which stood near the main line of tetrapod evolution." However, he does not present the evidence on which the statement is based.

Recently, while examining the crossopterygian material in the American Museum, we found two specimens of *Eusthenopteron foordi* Whiteaves, in which a portion of the vertebral column was quite well preserved. At first, we also thought the column was

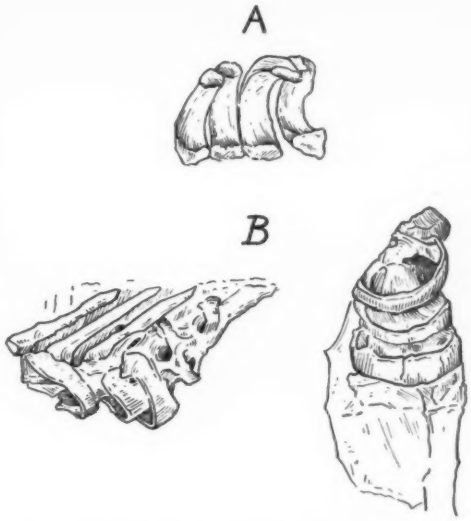

FIG. 2.—A, *Megalichthys nitidus*, ventral half-rings of four anterior centra. B, *Megalichthys nitidus*, lateral view of posterior centra and neural arches and ventral view of the same centra.

embolomerous but when the specimens had been cleaned up and X-ray photographs, taken by the Westinghouse Electrical Company, were made we found that this was not the case.

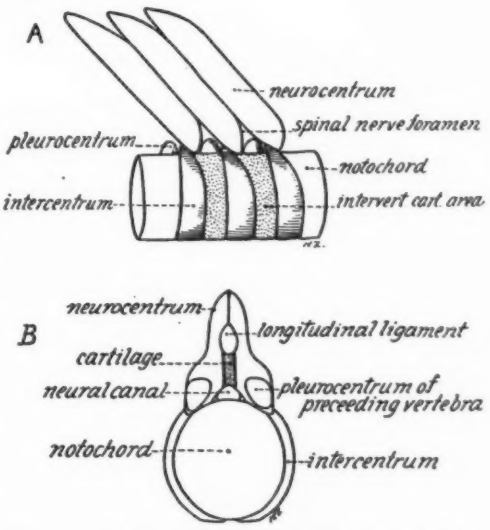

FIG. 3.—Diagrammatic representation of *Eusthenopteron* vertebrae. A, lateral view; B, front view.

The vertebral column (figs. 3, 4) instead of being embolomerous is quite similar to Gadow's schematic diagram of the vertebrae of the sturgeon (2). The centra consist of two crescentric half-rings that are separate both dorsally and ventrally. These half-rings are mere bony shells around a large notochord and are not thickened dorsally as Bryant stated. Ventrally each half-ring has a smooth, flattened, shiny surface that appears as if it may have been in contact with a membranous structure during life, possibly the dorsal surface of the air bladder, which is known to have been quite large in some crossopterygians.

Dorsally each half-centrum articulates with a large, well-developed neural arch and spine, which is quite wide anteroposteriorly. Between the bases of the neural arches and above the notochord is a pair of small rounded bony interdorsal elements, one on each side.

The intercentral areas beneath these interdorsal elements were presumably cartilaginous and, as Hussakof noted in the Albany specimen, which we have also examined, they increase in width posteriorly until in the mid-body region they are about the same width as the centra.

Following Gadow's terminology we have called the neural arch and spine the basidorsal, the small element between the bases of the neural arches the interdorsal, and the centrum the basiventral. In paleon-

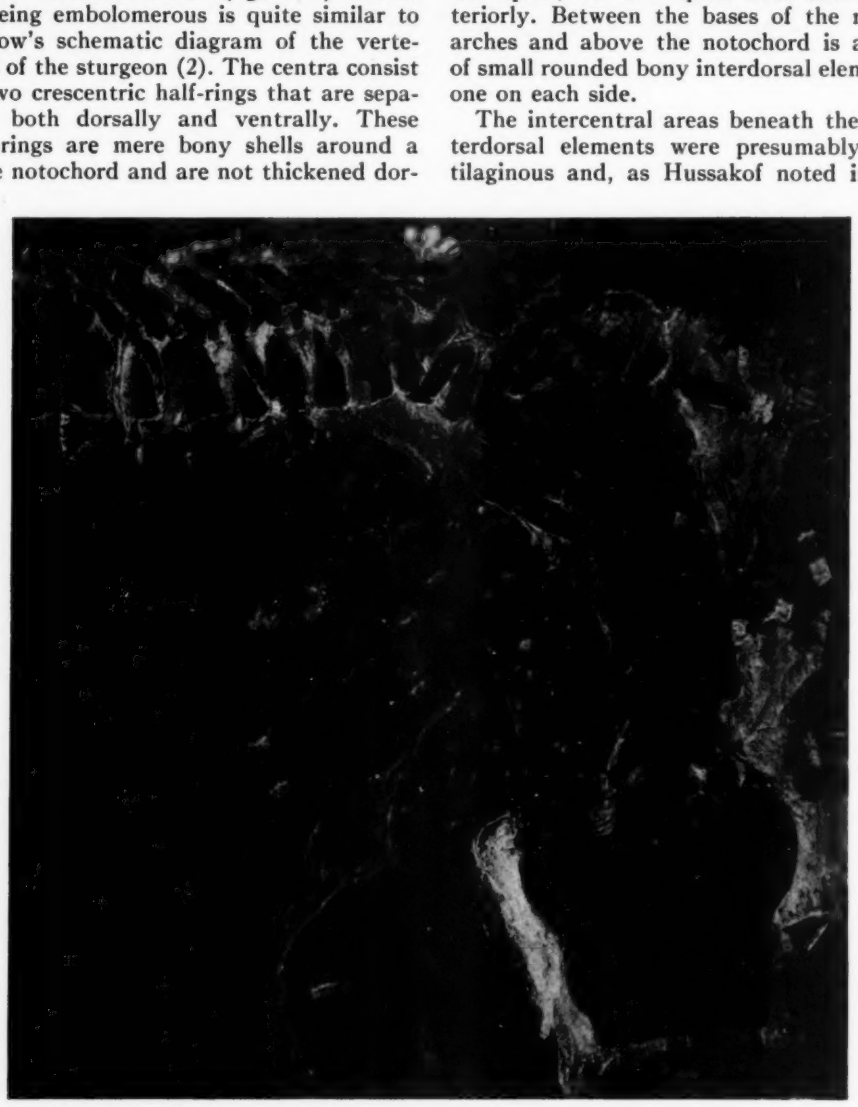

FIG. 4.—Photograph of part of the vertebral column of *Eusthenopteron foordi* Whiteaves.

tological terms the basidorsal equals the neurocentrum, the interdorsal equals the pleurocentrum and the basiventral equals the hypo- or intercentrum.

The vertebral column of *Eusthenopteron* is thus seen to be an ideal type from which the embolomerous vertebrae of the earliest amphibians can be derived either by ossification of the intervertebral cartilaginous space, or by the down-growth of the interdorsal element (pleurocentrum) to form a second ring around the notochord, or by a combination of these two processes.

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SIGNIFICANCE OF TERTIARY MAMMALIAN FAUNAS IN HOLARCTIC CORRELATION WITH ESPECIAL REFERENCE TO THE PLIOCENE IN CALIFORNIA

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ABSTRACT—The epochs of a period in the Tertiary time scale are, supposedly, convenient terms of expression, and Lyell's original designations have been altered somewhat by different authors. Many controversies have arisen over the arbitrary assignment of boundaries to these divisions. This article is concerned with the Mio-Pliocene boundary, particularly in California.

From a study of certain living mammals, it is recognized that similar fossil forms realized a wide and rapid dispersal without appreciable evolutionary change and are useful in holarctic correlation. Furthermore, the evidence shows that different plant associations were not effective barriers to these mammals. Hence it is again suggested that the equid genus *Hipparion* be accepted as an indicator of the beginning of the Pliocene.

The late-Tertiary time scale now in use on the Pacific Coast is based on the early identifications of fossil vertebrates from the Coalinga area in California and in part on the percentage methods as applied to the invertebrates. But the teeth of the horse *Neohipparion molle* Merriam from the Jacalitos, which were used to mark the beginning of Pliocene time on the Pacific Coast, are very close in structural characters to Middle Pliocene forms elsewhere in America. From the evidence now available, and in accordance with the above principles in intercontinental correlation, it is suggested that Pliocene time in California began with the Orinda, Lower Chanac, Upper Nerola and their equivalents.

NO SUBJECT has caused more comment and discussion in paleontology than the identification of epochs and periods as represented by the various formations and faunas. As additional evidence appears the old faunal breaks become less distinct and disappear through intergrading faunas, and many stratigraphic breaks are now considered of merely local significance. Indeed, in some instances, we find faunas representing two epochs within one formation. Although one may understand the sequence and evolutionary progress of the faunas, it is sometimes difficult to place certain faunas in their respective epochs due to the necessity of arbitration in defining the epochs.

In 1833 when Lyell and Deshayes first divided the Tertiary deposits into a chronological series of formations, they introduced the terms Eocene, Miocene, Older Pliocene and Newer Pliocene as convenient terms of expression in discussing the "periods" or epochs with which they were dealing. The publication of the first edition of volume 3 of Lyell's *Principles of Geology* was delayed about five years to include new and additional information. Lyell realized the necessity of changing his system of nomenclature for more practical usage. This was illustrated in 1873 when he adopted Edward Forbes' (1846) usage of his (Lyell, 1839) term Pleistocene for Post-Pliocene instead of Pleistocene for Newer Pliocene [=Sicilian only] as it was originally defined. If we were to apply strictly the rules of priority as used in biological nomenclature today, Pleistocene would be a synonym of "Newer Pliocene." But Pleistocene is accepted as an epoch and there is nothing gained by restricting it to its original usage.

In reviewing Lyell's *Principles of Geology*, we note that the Pontian and Sarmatian or their equivalents were not definitely included in the original scheme of chronologic succession. Subsequent investigation disclosed that these stages and their faunas occurred stratigraphically somewhere between the type Miocene of Superga Hill and the type Pliocene of the sub-Appenine

strata of northern Italy. Most invertebrate paleontologists have attempted to define the Tertiary epochs by the transgression and recession of the sea in western Europe. Thus, Stefanini believes that the sedimentary cycles in that area, as initiated by the beginning of transgression, should mark the commencement of an epoch, and the ultimate end of recession, its close. Unfortunately, the diastrophism affecting these movements of the sea can not be proven to be epeirogenic; furthermore, the invertebrate faunas in these formations did not range throughout the Holarctic Realm. Thus we note the possibility of error for interregional correlation in using either of these lines of evidence. On the other hand, vertebrate paleontologists have considered the appearance of new faunal assemblages (e.g., "Burdigalian," "Pontian," and "Astian") as the inceptions of new faunal cycles and these have been used by some authors as the most logical beginnings for the Tertiary epochs. But, as pointed out by Teilhard (1934, p. 288), " . . . such boundaries frequently do not coincide exactly with the limits of the marine transgression and regressions."

There have just appeared other papers (Tobien, 1938; Stolley, 1938) emphasizing further the persistent disagreement among European paleontologists and stratigraphers on the much discussed Mio-Pliocene boundary. Tobien directs attention to some new finds, reviews again the previous records, and argues for a Sarmatian and Upper Miocene age for the first Hipparions in Europe, although von Koenigswald (1931), Stromer (1937) and others have already defended a Lower Pliocene age of these records. After reviewing most of the evidence, Stolley insists that there is no positive proof for restricting *Hipparion* to the Pontian and states that an exhaustive reinvestigation is necessary.

There is no particular reason from Lyell's original designations for assigning the Sarmatian to either epoch. Since the boundary between the Miocene and Pliocene must be arbitrarily fixed, why not use the first appearance of *Hipparion* as the criterion to be used? This phenomenon has already been suggested and is either directly or indirectly accepted in holarctic correlation. It has the additional advantage of offering a more equal time division for the epochs in question.

The first appearance in any given region of these hipparions would necessarily be in small herds, as Stolley suggests, though in a relatively short time a maximum population for the species would be established. Thus tremendous herds could be produced in southeastern Europe within a score or two of years unless the environment or "ecologic niche"[1] was considerably restricted at the time of their arrival. In any event, if the first recorded hipparions from Eurasia are Miocene and those from the Pontian are Pliocene, differences should be reflected in the structure of the animals equivalent to those so clearly shown in American forms representing similar durations in time. To date no clear distinctions of this kind have been recorded.

It has been argued that the appearance of *Anchitherium* in both Miocene and Pliocene deposits of Europe tends to offset partly the value of *Hipparion* as a marker for the Pliocene (Stolley, 1938).[2] Before becoming involved in a discussion pertaining to the relative values of different genera as stage markers, the actual identification of the Pliocene "anchitherines" should be determined. Matthew has already called the Chinese form *Hypohippus zitteli*, and every comparison that can be made from the published illustrations indicates that they are nearer to the American hypohippines than to the European anchitherines. Thus they may have reached Eurasia at the time of the first hipparion invasion.

Similarly *Equus* has been suggested as a suitable marker for the beginning of the Pleistocene, but this is less applicable. Aside from shortening the Pliocene epoch, it would place part of the type Pliocene (Astian) in the Pleistocene and extend the Pleistocene back to include the faunas now considered

[1] Anyone interested in animal populations and their dispersal should read *Presence and Absence of Animals* by Joseph Grinnell, University of California Chronicle, pp. 429–450, October, 1928.

[2] Stolley (pp. 196, 197) stresses the fact that the *Hipparion* tooth supposedly from the Glimmerton from Morsum Cliff of Sylt, Denmark, was not found in the upper Miocene micaceous clay but on the beach. He expressed the opinion that it might very readily have come from beds higher up in the cliff. Certain facts are presented in support of his contention.

as Upper Pliocene. It therefore seems more practicable to consider the beginning of Pleistocene time as the first major advance of the glacial ice sheets, though the exact allocation of that event with reference to the geologic time scale is probably less determinable than the first appearance of *Equus*.

Land mammals have long been recognized as useful for intercontinental correlation. Many genera have undergone holarctic dispersal without any profound change in their species. But during the last fifteen years, there has been a strong tendency to invoke the principle of homotaxis[3] in holarctic correlation. On the other hand, evidence indicates that direct correlation between Eurasiatic and North American mammalian faunas can be made, at least within the limits of stages of an epoch. Comparison of the appended list of Recent mammals in the Holarctic Realm indicates that there has been a wide dispersal of genera, common to both continents, without any appreciable evolutionary change. Thus, it seems unnecessary to apply the principle of homotaxis in correlating the mammalian faunal ages, within the Holarctic Realm. Matthew (1913, p. 290) realized the significance of this rapid dispersal; to quote:

> These considerations [correlation of homotaxial ages of a phylum] have some bearing on the Tertiary horizons in Europe and the United States; but so much of our mammalian fauna is derived from dispersal centers more or less equidistant from these two regions that no serious error can ensue from neglecting them. . . .

A study of the relationships and the distribution of living mammals is one of our best clues to what may have occurred with Tertiary mammalian faunas. Most of us are familiar with the wide distribution of the bison, pronghorn, and deer in North America, and the dispersal of some other genera prior to the invasion of white men was even more far-reaching. Indeed, in surveying the Recent mammalian terrestrial genera of the New and Old World, we note that there are about 34 genera and subgenera representing five orders common to the two hemispheres. Then, if we inspect carefully the characters by which these *genera* are distinguished from their nearest relatives, we shall see that characters of equivalent rank are being used in describing fossil *species* today, and in some instances, with our scanty fossil representation, such differences would not even be recognized. Though some of the living mammals may be divided into subspecies, it is usually necessary to detect such differences by large series of skins and skulls; but such minor differences cannot be recognized in fossil mammals, due primarily to the incompleteness of the materials available for study.

The fact remains, then, that during Quaternary time different species of given genera have distributed themselves throughout the Holarctic Realm without any more, if as much, change as in the species of *Hipparion* from the Lower Pliocene of both hemispheres. And in the Pliocene, mountain and desert barriers were probably less formidable than in the Pleistocene and today. Thus it seems wholly unnecessary to presume that one-third of the Pliocene lapsed after the first appearance of *Hipparion* in America before it arrived in Europe. The wide distribution of such a rapidly evolving form within a relatively short time seems to be well supported from our knowledge of Recent mammals.

Paleobotanists, working with Tertiary plant remains, particularly leaves, have been using methods in correlation that differ markedly in some respect from the direct identification method in vertebrate and invertebrate paleontology. It is nevertheless recognized by these writers that certain age determinations must be derived from invertebrate or vertebrate evidence (Chaney, 1936, p. 319); then, given the latitude and altitude of other fossil floras, their position in the stratigraphic column can be determined. It is inferred that most of these leaf localities were in the lower valleys a few hundred or possibly a thousand feet above sea level at the time they were deposited. The following quotation will give a better understanding of this thesis:

> To many stratigraphers, the concept of a "Miocene" forest on the ridges or at high latitudes during the Eocene period is highly distasteful. Such a situation has given rise to the conclusion

[3] Faunas of similar character and scope containing the same groups in a similar stage of evolution may not be, necessarily, of identical age.

that Cenozoic plants are without value as time indicators. This is admitted as frequently the case, except as the latitude of the fossil plant occurrence is taken into consideration. But with an established climatic trend, based upon a known physical history of emergence and orogeny, the position of a Cenozoic flora with reference to the equator may indicate its position in the stratigraphic column as accurately as can the stage of evolution of a mammal or a mollusc. (Chaney, 1936, p. 320.)

This principle has been applied to fossil floras in California, Oregon, Nevada, Idaho and Washington, and attempts are now being made to extend it to other parts of the world. Furthermore, it has been suggested that if this principle were applied to vertebrate paleontology, we should find proper solution to many of our disagreements in correlation.

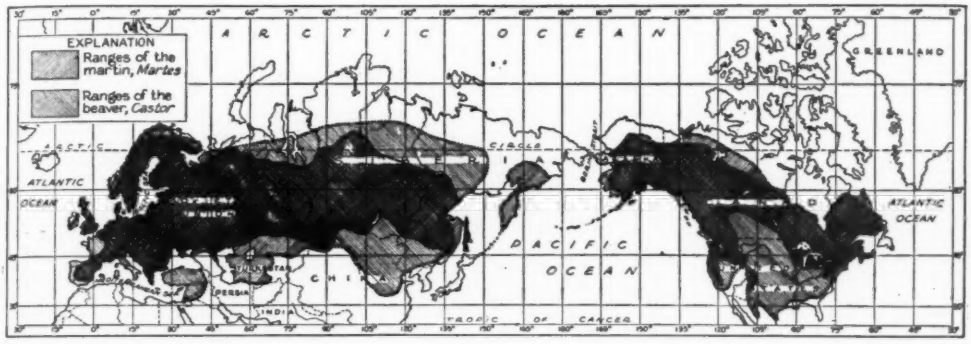


FIG. 1.—Holarctic distribution of the Eurasiatic martins, taken from OGNEV, S.I. *1928, Animals o Eastern and Northern Asia*, vol. 1, p. 757, Govt. Publ. House, Leningrad; the American martins from E. T. SETON, 1929, vol. 2, part 2, p. 485. The beaver distribution is compiled from various reports on the Pleistocene and Recent faunas.

One glance at the distributional maps, figures 1 and 2, as well as further reference to the ranges of Recent Mammalia, will show that many of the genera and species of larger mammals are dispersed through several plant zones and over mountain and desert barriers. To quote Seton (1929, vol. 3, p. 418),

> The antelope [*Antilocapra*] is essentially a creature of the open country, a product of the wide and arid or semi-arid Plains or adjacent foothills. Yet it was found in parks or treeless plains high in the mountains, even when to reach these, it had perforce to journey through woods and rugged passes.

Likewise our bighorn sheep, normally restricted to the high and precipitous, mountainous areas, are not infrequently encountered in intermontane regions, sometimes barely within sight of their customary range. Thus we see that over-population or other stimuli effecting the spread of mammal populations would occasion rather wide dispersal even over supposed barriers to other suitable areas of occupation. One species of Recent weasels, *Mustela frenata*, ranges from Peru to British Columbia, throughout the United States, Mexico and Central America (Hall, 1936, p. 101). On the whole, then, it would seem a bit misleading to apply these paleobotanical principles of correlation to Tertiary mammals.

It is reasonable to presume that the species of Tertiary mammalian faunas ranged as freely, if not more freely, through the different plant zones as the related species or species of similar habits today. Such wide-ranging forms, therefore, have been recognized as valuable evidence in long-range correlation. While it is felt that Foraminifera and molluscs are best suited for close zonal determinations within limited areas, the mammalian evidence is best applied to the determination of stages in continental and intercontinental correlation. Plants are more useful as climatic indicators.

American beavers show an intergradation between the upper Miocene genus *Monosaulax* and the lower Pliocene *Eucastor* in the later upper Miocene Niobrara River fauna from northern Nebraska. Then the

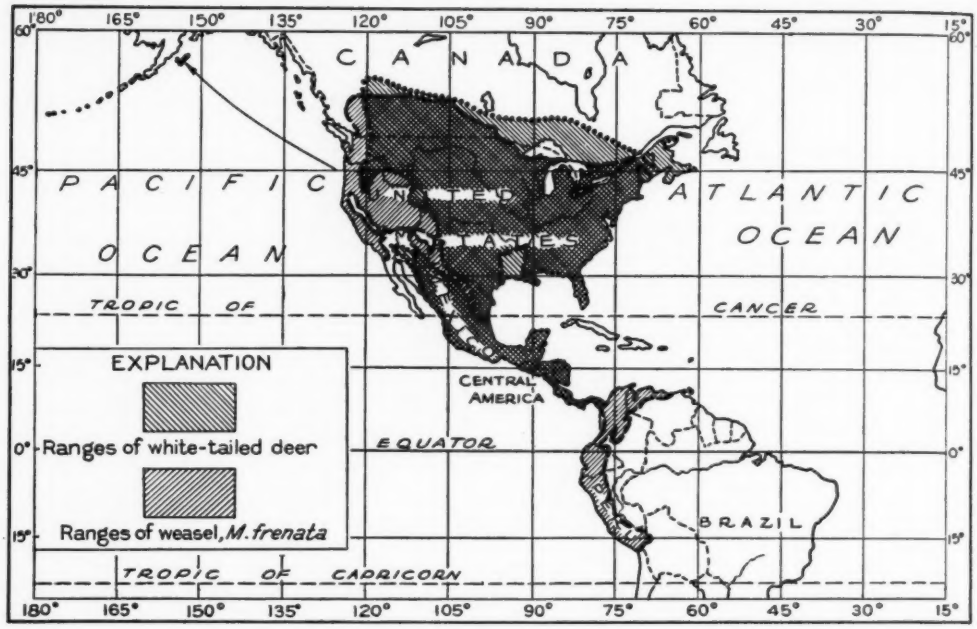


FIG. 2.—American distribution of white-tailed deer, taken from E. T. SETON, *1929*, vol. 3, part 1, p. 241. Though these deer extend far into South America, the information available is insufficient to show the limits of their range on the map. Range of *Mustel frenata* after E. R. HALL, *1936*, p. 101.

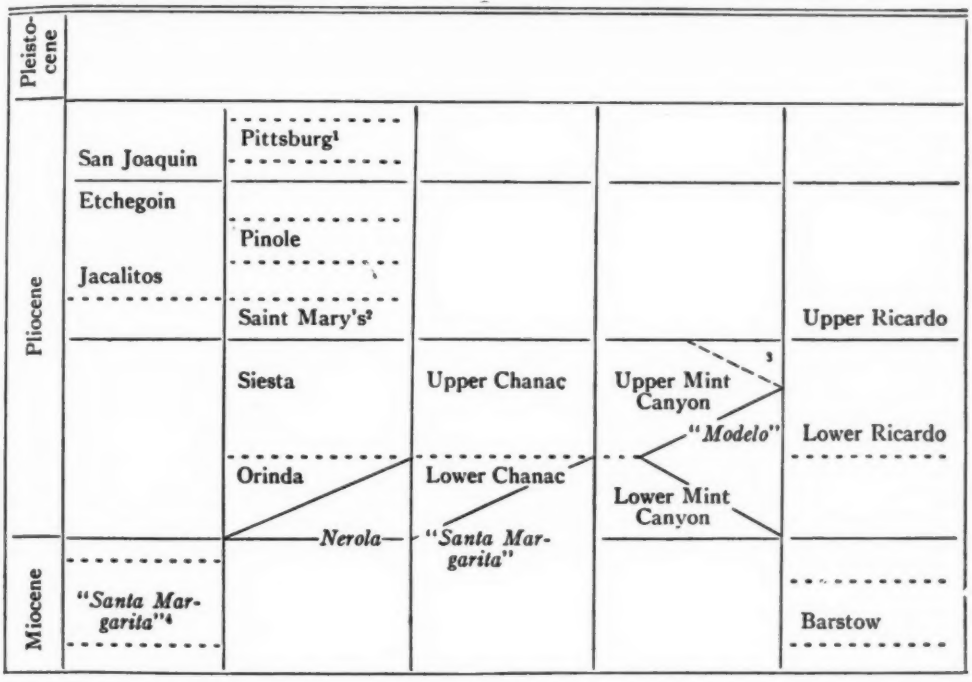
species of *Eucastor* became widely distributed in the American lower Pliocene, though they did not reach Eurasia. At the close of that stage, they gave rise to *Dipoides*. The species of *Dipoides*, in turn, not only replaced those of *Eucastor* in middle Pliocene time, but the different species dispersed themselves throughout the holarctic realm. Now, in accordance with the principle of homotaxis, if *Dipoides* made its first appearance in the middle Pliocene of America, it should appear in the upper Pliocene of Eurasia. On the contrary, it has been found only in beds older than those referred to the upper Pliocene in the Old World, substantiating further the intercontinental correlation based on other mammalian evidence.

Prior to 1915, there was little or no information on the relative age of marine and terrestrial faunas on the Pacific Coast. In 1913 some vertebrate remains, principally horse teeth, were found in the Coalinga district, and subsequently reported by J. C. Merriam (1915). It was through these determinations and correlation, together with the percentage method as applied to the invertebrates, that most of the present Mio-Pliocene time scale of the Pacific Coast originated. At that time the distinctions between the lower, middle, and upper Pliocene vertebrate ages were not recognized in America. The occurrence of a *Hipparion*-like form was hailed by most paleontologists as indicating a lower Pliocene age. Thus *Neohipparion molle*, though it is practically identical with middle Pliocene elsewhere in America,[4] together with a *Pliohippus* tooth was the evidence used in referring the Jacalitos[5] to the lower Pliocene. Consequently the underlying "Santa Margarita," which is separated from the Etchegoin sands (Etchegoin+Jacalitos) by an unconformity, was considered as Upper Miocene.

[4] Compare with *Neohipparion eurystyle* (Cope ?Goodnight and Hemphill of Texas; *N. phosphorum* (Simpson), Alachua, Florida; *N. leptode* Merriam, Thousand Creek, Nevada.

[5] Gester and Galloway (1933) now consider the Jacalitos as part of the Etchegoin formation.

CORRELATION OF SOME VERTEBRATE AND INVERTEBRATE FAUNAS IN CALIFORNIA



Vertebrate faunas in roman, invertebrate faunas in italics.

[1] See Stirton, 1938, in press.

[2] See Stirton, 1938, in press.

[3] The exact stratigraphic relations of the "Modelo" to the vertebrate horizons in the Mint Canyon area have not been established (see footnote 7).

[4] The age relationship of the "Santa Margarita" north of Coalinga has not been definitely accepted. The upper part may be equivalent to the upper Nerola, but recent investigations in that area by oil geologists tend to place it farther down in the section.

During the past few years, however, we have discovered *Nannippus tehonensis* (Merriam), a lower Pliocene species (Stirton, 1938, in press), in the Nerola and Orinda in the San Francisco Bay region. Previously it had been found in the lower Chanac and in the top of the "Santa Margarita" at the southern end of the San Joaquin Valley (Stirton, 1938). Though no unquestioned *Hipparion* (*strictu sensu*) has been found in the Orinda fauna, some fragments suggest its presence. Most of the *Hipparion* teeth on record from California seem to be of Siesta or later age, and this includes those from Mint Canyon[6] (Stirton, 1933), Ricardo, and the tooth from the Puente (Stock, 1928). It may be argued that since there is no definite evidence of *Hipparion* in the Orinda, the difference in age is sufficient to place that formation in the upper Miocene. But the evidence tends to show that the Orinda fauna is equivalent in age to the first appearance of *Hipparion* in Europe, and the evidence for the presence of *Hipparion* in the Orinda (Stirton, 1938), together with forms of equal advancement, *Nannippus* and *Pliohippus*, can not be discounted. Thus we see that the correlation of these Pacific Coast faunas is based on the approximate simultaneous appearance of *Hipparion* in these beds and in the Sarmato-Pontian of Europe and not on a comparison with forms from the Great Plains as stated by Condit (1938, p. 243); though such comparison as can be made with Great

[6] Maxson's (1930) fig. 7 evidently is *N. tehonensis* and since it was found in the lower part of the Mint Canyon beds may be of Orinda age.

Plains faunas likewise indicates a lower Pliocene age for the Orinda and upper part of the Nerola. Therefore, those who correlate the beginning of the Pliocene with the first appearance of *Hipparion* and contemporaneous forms find approximately a stage difference in time between a direct correlation based on terrestrial vertebrates and that now commonly in use on the Pacific Coast. But it should be stressed that any disagreement in the time scale drawn here and the time scale now in use on the Pacific Coast does not involve any discrepancy in the stratigraphic position of the vertebrates and invertebrates.

It has been thought that the Mint Canyon and the overlying "Modelo" in that area was an exception. Evidence recently disclosed by Kleinpell (1938, p. 71), however, indicates that the "Modelo" in the Mint Canyon area is not older than the Nerola, and there is some proof that it might be slightly younger. Unless more accurate information can be obtained for the Puente *Hipparion* tooth (Stock, 1928) or some definite association can be made with an invertebrate fauna (see Kleinpell, 1938), it would seem irrelevant to discuss that occurrence more at this time.

Certain vertebrate paleontologists in America apparently are influenced by the correlations based on invertebrate evidence, though they fail to recognize the fact that the basis for these correlations was an incorrect application of the wide and rapid dispersal of *Hipparion*. It has been tactfully suggested that the vertebrate time scale should be altered to coincide with that of the invertebrates. This procedure will only add confusion to future attempts in establishing synchrony of world-wide events in the geologic past. It seems advisable to consider all evidence available in such correlation with especial emphasis on rapidly dispersing and wide-ranging animals.

RECENT GENERA OF TERRESTRIAL MAMMALS COMMON TO NORTH AMERICA AND EURASIA

Insectivora
  Sorex
Carnivora
  Ursus
  Thalarctos
  Martes
  Mustela
  Felis
  Lynx
Lagomorpha
  Ochotona
  Lepus
Artiodactyla
  Cervus
  Alces
  Rangifer
  Bison
  Ovis
Rodentia
  Marmota
  Citellus
  Eutamias
  Sciurus
  Tamiasciurus—subgenus
  Glaucomys = Pteromys
  Castor
  Microtus—subgenus
  Lemmus
  Dicrostonyx
  Cleithronomys
  Lagurus
  Zapus
  Lutreola—subgenus
  Putorius—subgenus
  Gulo
  Lutra
  Vulpes
  Alopex
  Canis

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JOURNAL OF PALEONTOLOGY, VOL. 13, NO. 1, PP. 137–139, JANUARY, 1939

CERTAIN POSSIBILITIES IN THE FIELD STUDY OF VERTEBRATE FOSSILS

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ABSTRACT—Population studies in the field indicate a very high infant and adolescent death rate in *Mesohippus*, and apparently indicate a very critical time in equine history during the Oligocene. Similar observations on titanotheres seem to show that their extinction occurred during a hiatus in deposition, as the infant and adolescent death rate is very low among preserved specimens.

ALL PALEONTOLOGISTS are aware that collections from abundantly fossiliferous horizons represent only a very small proportion of the total number of specimens in the field. Furthermore, for obvious practical reasons, the specimens collected are either very complete and perfect or else fragments of extremely rare forms. Such criteria of collection are natural and practical, but, since they establish as standards either perfection of preservation or rarity, the resulting assemblages frequently differ in proportion from the natural populations represented in the field. With these facts in mind, it seems necessary to study relative numbers and other ecological data directly in the field, as the collection of all the bone exposed, for instance, in even one square mile of the Brulé in the South Dakota badlands would be impractical and almost impossible.

In an effort to determine the possibilities of the field study of vertebrates, I have during the past field season made observations on the occurrence of *Mesohippus* in the lower nodular zone of the Brulé of the Big Badlands, and have compared them with similar observations on the Chadron titanotheres made during the field seasons of 1932–1934. The results seem to indicate certain points not previously known in the history of the two groups. It is hoped that this paper will induce others to check them, both in the Big Badlands and elsewhere.

The skull of *Mesohippus* is, as all collectors know, extremely delicate, and usually occurs dissociated in the entombing sediment. Ankylosis due to increasing age

strengthens the sutures, so that most of the skulls suitable for collection are those of individuals fully adult or old-aged at the time of their death. Oreodonts, on the other hand, had very well knit skulls, which frequently were buried in perfect condition. Therefore, although the proportion of scraps of *Mesohippus* to scraps of *Oreodon* in the field is about one *Mesohippus* to ten or fifteen *Oreodons*, the disproportion in numbers of good specimens is much greater.

Allowing as well as possible for the fact that one *Mesohippus* usually occurs in several pieces, and that pieces of several *Mesohippi* might easily occur in one place, I have observed scraps representing between two and three hundred individuals in the lower nodular zone. Of this number, approximately one-fourth were animals with the third molar not yet fully erupted, and the rest were adult or senile. The absence of very young colts is almost certainly an accident of preservation, due to extreme delicacy of the bone and the activity of large contemporaneous carnivores rather than to a low infant mortality.

In any normal group, the period of late adolescence and early maturity is the time of greatest physical vigor, greatest resistance to disease, and, ordinarily, lowest death rate. As it is always a time of death rate lower than that of infancy and childhood, it seems safe to infer that at least as many *Mesohippi* died in infancy as in early maturity, in spite of the absence of preserved specimens. Therefore, it seems probable that approximately two-fifths or one-half of all the *Mesohippi* born in the area during lower Brulé time died before they had more than well started their reproductive life. Such a death rate might not be serious among forms such as the rabbits, where large litters are the rule, but in a perissodactyl, where all the evidence of recent representatives indicates the production of one, two, or at most three young at a birth, it almost certainly would be.

Observations on *Mesohippus* were extended to the upper Brulé (*Leptauchenia* beds) in an effort to determine the later equine history of the area, with somewhat surprising results. Although oreodonts abound at many horizons through the *Leptauchenia* beds, horses occur almost not at all. One rather good specimen and two scraps were all I could find, despite a profusion of oreodonts and other forms indicating a continuance of essentially the same geographic environmental conditions as obtained during lower Brulé time, when horses and oreodonts occurred in abundance together. Cursory examination of the literature indicates that the several species of *Mesohippus* and *Miohippus* described from the Big Badlands are based usually upon single scraps, and the total number of upper Brulé individuals represented in collections probably does not exceed thirty.

The extremely high infant and youthful death rate of the lower Brulé *Mesohippi*, coupled with the rarity of equine remains in the otherwise abundantly fossiliferous upper Brulé, seems clearly to indicate that the Brulé sediments record a time critical in equine history, at least in the area studied. The causes of extinction of a previously self-maintaining species or genus within any area may conveniently be divided into three possibilities: (1) Mass migration out of the area; (2) Decrease in birth rate (operative usually in groups already badly depleted by other factors, e.g., the passenger pigeons, certain Indian tribes of the American Southwest, certain Eskimo tribes, and several cases among the Bovidae); (3) Increase in death rate, especially in the younger age groups.

Plainly, some factor or factors attributable to the third class of causes were operative in the case of *Mesohippus*. As the lithology and faunas give evidence of essentially the same geographic and climatic environmental conditions lasting from the upper Chadron through the upper Brulé, and as the other herbivorous forms contemporaneous with *Mesohippus* do not show signs of undergoing similar difficulties, it is probable that the unfavorable factor was pathologic rather than climatic. Whether the pathology was infectious, parasitic, or genetic in nature is, of course, indeterminable at present.

In striking contrast with the condition in the Brulé *Mesohippi*, almost all of the Chadron titanotheres of the Big Badlands are fully adult or senile. Estimating very conservatively, there are at least three hundred skulls in the various collections. As nearly as can be determined from the

literature, less than ten of the collected specimens represent infantile or adolescent individuals. During stratigraphic studies of the Chadron formation, I have had the opportunity to examine skulls and other bones belonging to at least two hundred more. It is difficult to be sure how many individuals are represented in any of the great "graveyards" of bone in the Chadron, but making allowances for this, I have seen approximately ten cases of immature bone in the total of two hundred mentioned.

This is more impressive from the fact that titanothere skulls, even in infancy, were sufficiently well knit to tend not to disintegrate before burial, and the limb bones and vertebrae were too massive for destruction by carnivores. Therefore, the chances for preservation of young individuals were immeasurably better than in the case of *Mesohippus*, and the small number of juvenile specimens must indicate that most of the animals born had lived through most of their reproductive life.

At first sight, such an idea might seem incompatible with the extinction of the titanotheres; however, the key to the apparent anomaly lies in the stratigraphy of the Chadron formation.[1] Practically all of the titanotheres in collections and those that have been studied in the field occur in the middle member of the Chadron; the upper member is almost devoid of them. A slight but significant hiatus in deposition occurs between the middle and upper members, and in that time the titanotheres suffered their great depletion. During the time when most of the specimens were being buried the race was successfully maintaining itself, and while the race was being destroyed no specimens were being preserved. Other interpretations are possible, but this seems, on the whole, the most conservative.

In conclusion, it must be understood that this paper is intended merely as a suggestion of a few possibilities; it by no means exhausts them. An accumulating mass of data from quarry sites and assemblages from restricted horizons raises the hope that we may in the future be able to assign many fossil forms to definite ecologic stations within their ranges, to study the causes of their extinction, and to learn in detail the "natural history" of their time.

[1] Clark, J., *1937*, The stratigraphy and fauna of the Chadron formation in the Big Badlands of South Dakota: *Carnegie Museum Annals*.

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JOURNAL OF PALEONTOLOGY, VOL. 13, NO. 1, PP. 139–140, JANUARY, 1939

STATUS OF THE OLIGOCENE INSECTIVORE GENUS METACODON

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ABSTRACT—The revised description of the genus *Metacodon* by Patterson and McGrew is confirmed, and the restoration of the jaw angle of the genotype specimen is declared inexact.

THE GENUS *Metacodon* was named and described by me in Scott and Jepsen's "Monograph on the mammalian fauna of the White River Oligocene, Part I." (1) The genotype species is *Metacodon magnus Clark*, and the type and only specimen when described was a partial lower jaw, with P_4, $M_{1,2,3}$, Princeton Museum no. 13,835. It was referred to the Leptictidae on the basis of the close resemblance to

Leptacodon Matthew and Granger, particularly to *L. packi* Jepsen. Characters separating it from *Leptacodon* were "the extreme reduction of the angle and lowering of the condyle."

On December 28, 1937, Patterson and McGrew published (2) a discussion of *Metacodon* with description of a new species, *Metacodon mellingeri*. They referred the genus to the Erinaceidae rather than to the Leptictidae, and gave a revised generic diagnosis based on material much more complete than the genotype. Also they stated that the reduction of the angle and lowering of the condyle in the genotype can not be regarded as established because

The holotype was found in fragments, and the contacts in the posterior region, although apparently good were found on close re-examination to be inexact. This matter will be discussed by Dr. Clark in his forthcoming paper on the Chadron beds.

In regard to the contacts on the genotype specimen, Patterson and McGrew are entirely correct. Mr. Patterson, Professor Jepsen and I studied the specimen together and found that the fragments of which the angle was composed were so small and thin that they would make apparent contacts in almost any position. The original restoration is definitely inexact, and the characters mentioned probably are indeterminable in the type specimen. At the time when we discovered this fact, the paper on the Chadron (3), which repeats the original description, was too far advanced towards publication to be corrected.

Patterson and McGrew referred *Metacodon* to the Erinaceidae chiefly because of the absence of molarization in P^4. They regard the structure of the ectoconal shelves and the paracone-metacone position on M^{1-3} in Metacodon as fundamentally erinaceid and very different from leptictid conditions. They consider *Proterix* as probably an erinaceine, and as such more advanced structurally than some of the living echinosoricines with which they made comparisons. As they were working with both upper and lower dental series, whereas my original reference to the Leptictidae is based entirely on a partial lower dentition, their evidence is very much more conclusive than the original was. However, though admitting this freely, I am not yet ready to commit myself on the family relationships of *Metacodon*. It seems better at present to hold definite family reference in abeyance until the Oligocene erinaceids are better known, for *Metacodon* resembles *Proterix* even less than it does the leptictids.

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